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PLANKTON OF THE FLORIDA CURRENT. II. SIPHONOPHORA¹

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ABSTRACT

Siphonophores present in the Florida Current off Miami have been studied for 18 months. The seasonal distribution of each species is described together with its vertical distribution, diurnal migration and cycle of alternation of generations. When comparison has been possible, results agree fairly well with those from the Bermuda area. It was shown that, superimposed on seasonal fluctuations in numbers, most species vary somewhat in relation to the water mass present. In this locality, water mass change is associated with temperature changes. The siphonophores as a whole adjust their day level in relation to the temperature.

Since 1950, a study of the plankton of the Florida Current off Miami, Florida, has been in progress with the assistance of a grant from the National Geographic Society. A first report on the hydrographic conditions encountered during the work has already appeared (Miller, Moore and Kvammen, 1953). Methods used in the collection of the plankton have also been described in that report. The present paper is one of a series on different groups of the zooplankton. The only previous study of the seasonal distribution of oceanic zooplankton in the North Atlantic is that for the Bermuda area (Moore, 1949). The siphonophores from Bermuda, a representative series of which had been identified by Dr. A. K. Totton, were available in the present work and were taken as a standard of comparison, the only species encountered here, but not in Bermuda being *Enneagonum hyalinum*. A few changes in nomenclature have, however, been made at the suggestion of Dr. M. Sears.

It was hoped that the present study would provide an amplification of the Bermuda work and allow the verification of some of the generalizations that were made there on such relationships as vertical distribution and illumination. For much of this comparison, it will be better to await publication of the results on other groups, and thus utilize a greater number of species. The data necessary for such

¹Contribution No. 86 from the Marine Laboratory, University of Miami.

comparison is therefore presented briefly here and will not be discussed at present. Complete tabulation of the results from all hauls is filed in the library of the Marine Laboratory. The results discussed more fully here are those which are characteristic of particular species rather than of zooplankton as a whole.

LIST OF SPECIES

The following species were recorded during the work. Details with regard to the commoner ones are given later, but some notes are appended here to those which were found only in small numbers.

Amphicaryon acaule Chun

Agalma spp.

Detached bracts and nectophores were taken occasionally but were not specifically identified. They were not common.

Hippopodius hippopus Forskål

Abyla trigona Quoy and Gaimard

Small numbers were taken in the autumn and winter of both years.

Abyla leuckartii Huxley

Abylopsis eschscholtzii Huxley

A. tetragona Otto

Enneagonum hyalinum Quoy and Gaimard

Bassia bassensis (Quoy and Gaimard)

Diphyes dispar Chamisso and Eysenhardt

D. bojani (Eschscholtz)

Eudoxoides spiralis (Bigelow)

E. mitra (Huxley)

Chelophyes appendiculata (Eschscholtz)

What was presumed to be the eudoxid generation of this species was taken fairly commonly in Bermuda but was seen on only one or two occasions in Florida waters, despite the comparative abundance of the polygastric generation there.

Lensia subtilis (Chun)

L. fowleri (Bigelow)

L. campanella (Moser)

L. cossack Totton

Sulceolaria monoica (Chun)

Single specimens occasionally throughout the year.

Galettia australis (Quoy and Gaimard)

Single specimens occasionally in winter and spring.

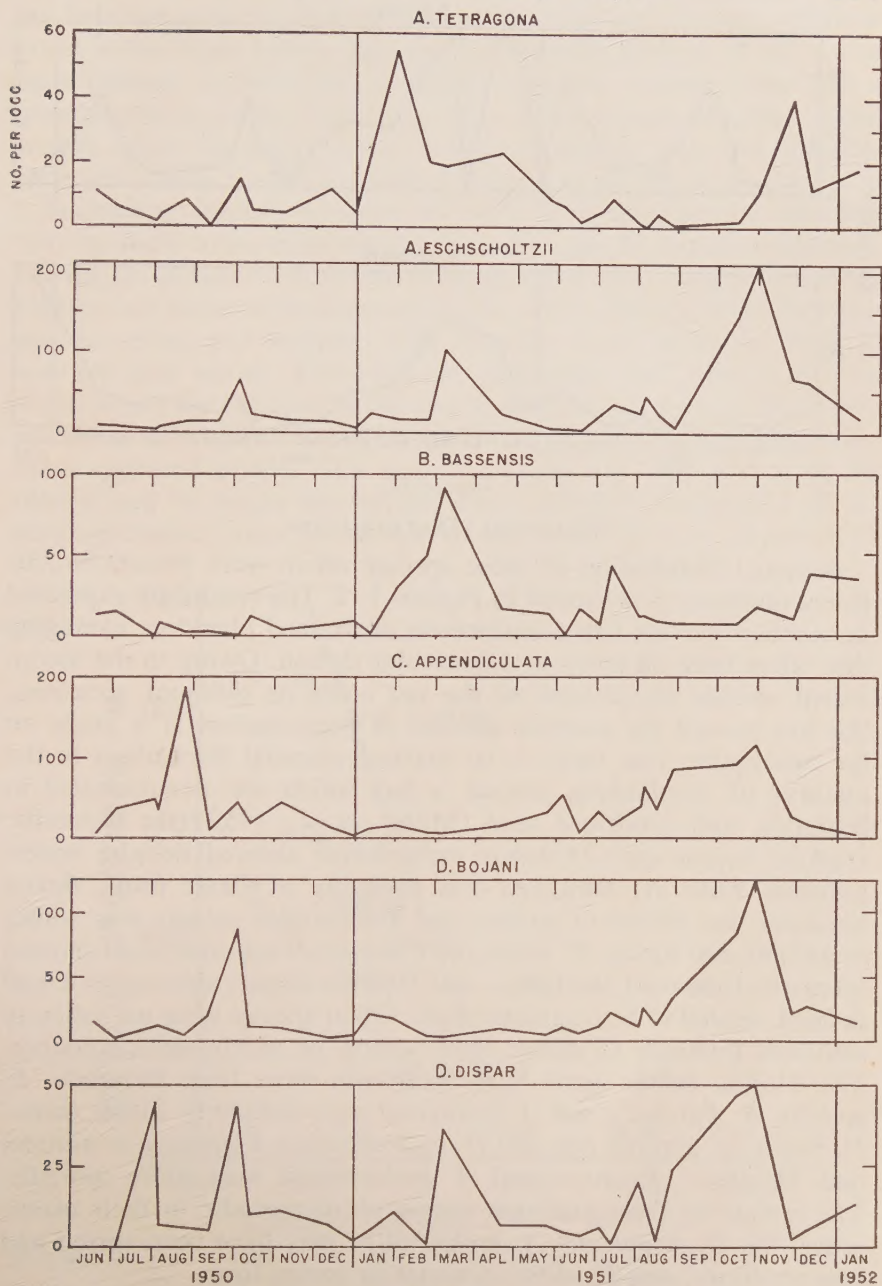


Figure 1.

FIGURES 1, 2. Seasonal distribution.

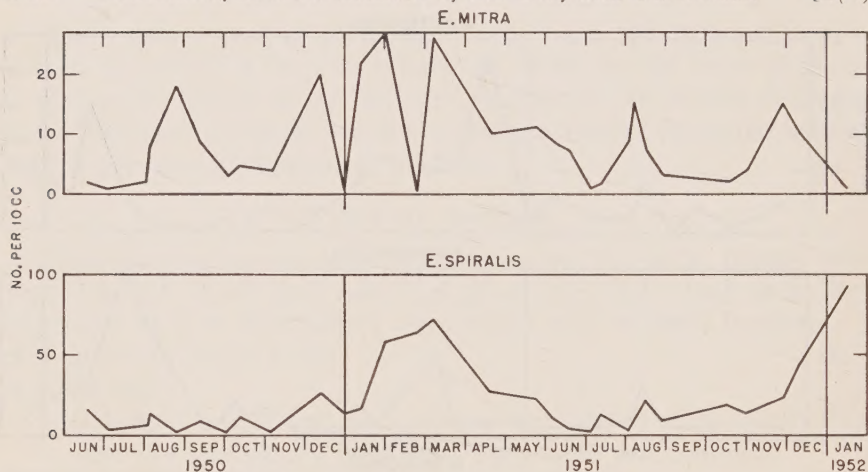


Figure 2.

SEASONAL DISTRIBUTION

Seasonal distribution of those species which were present in sufficient numbers, is presented in Figures 1, 2. The results are expressed as numbers per ten cubic centimeters of drained plankton, averaging that taken from all levels at a particular station. Owing to the inconsistent vertical distribution of the net hauls on different occasions, this has proved the simplest method of presentation. It is made on the assumption that there is no marked seasonal fluctuation in the quantity of zooplankton present, a fact which was demonstrated in Bermuda, and confirmed here (Miller, *et al.*, 1952). In Bermuda, *Diphyes bojani* and *Abylopsis eschscholtzii* showed definite winter maxima, while *A. tetragona* was probably a winter form, *Bassia bassensis* was winter or spring, and *Eudoxoides spiralis* was winter or autumn and spring. *E. mitra* and *Chelophyes appendiculata* showed no marked seasonal maximum, and *Diphyes dispar*, although not well defined, tended to be a summer form. Other species were not taken in sufficient numbers to define their season of maximum abundance. The Florida results agree fairly well with those from Bermuda. *E. spiralis*, *B. bassensis* and *A. tetragona* were definitely winter forms, *D. bojani* an autumn one and *D. appendiculata* a summer or autumn one. *D. dispar*, *E. mitra* and *A. eschscholtzii* were more sporadic. The remaining three common species were sporadic in their occurrence, but *D. dispar* and *A. eschscholtzii* may have been spring and autumn forms, and *E. mitra*, a winter or spring form.

In both the Bermuda and Florida areas, fluctuations in numbers

are believed to be in part due to inherent seasonal changes within a given water mass, but in part also to seasonal changes in the water mass present. In Bermuda, it appears that the summer water has a more northerly origin and brings with it forms typical of rather colder waters, while the winter water is more southerly in origin (Moore, Hela and Owre, in MS.). In the Florida current off Miami, there is a fluctuating amount of water of Gulf of Mexico origin intruding into the main water mass which comes through the Yucatan Channel. During the period of these observations, there was a general tendency for the Gulf water to predominate at the station being studied throughout the spring and summer, with Yucatan water taking its place in autumn and winter. However, the condition was complicated by short period fluctuations in the two water masses. As a further complication, in August 1951, and again in January 1952, a third water mass appeared briefly. This agreed in character with neither of the others, and its origin has not yet been definitely determined. If, as seems probable, some of our species are relatively more abundant in

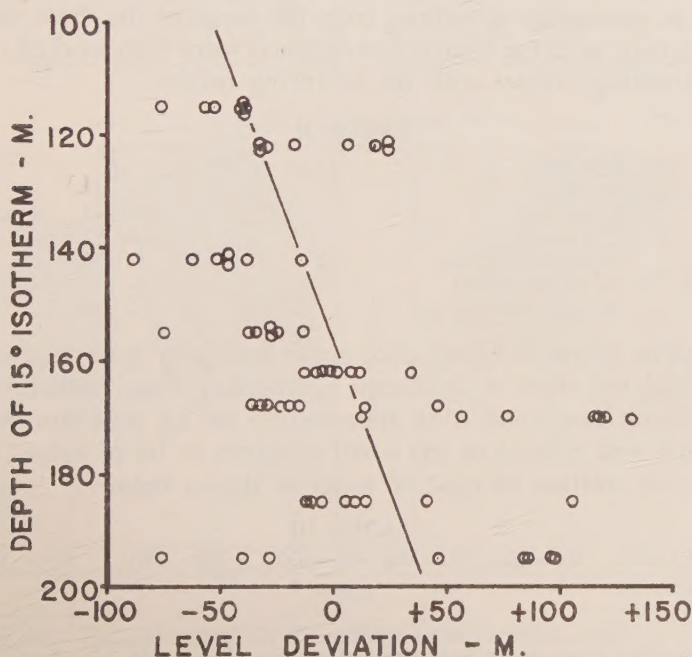


FIGURE 3. The deviation, on different occasions, of each species from its mean day level for the whole period of observation, plotted against the depth of the 15°C. isotherm.

one water mass than in the other, then some of the observed fluctuations in abundance might be due to this, rather than to a seasonal cause. Correlation coefficients were calculated between abundance of the various species and the percentage of Gulf of Mexico water present (Table I).

TABLE I

<i>Species</i>	<i>r</i>
<i>D. dispar</i>	+ .47
<i>D. appendiculata</i>	+ .64
<i>E. spiralis</i>	— .46
Significant value at $P = 5\%$	.468
Significant value at $P = 1\%$	.542

For the remaining species the correlations were not significant. The seasonal variation was, however, so great, that it would obscure the water mass relationship in such a small series, and the following method was therefore used to eliminate seasonal effect. It was assumed that the same seasonal cycle occurred in the two water masses. The values for numbers and for percentage of Gulf water were expressed as percentage deviations from the mean of the three readings of which they were the center. Correlations were then worked out for these percentage values with the following results.

TABLE II

<i>Species</i>	<i>r</i>
<i>D. dispar</i>	+ .49
<i>E. mitra</i>	— .47
<i>E. spiralis</i>	— .57
<i>C. appendiculata</i>	+ .58
<i>A. eschscholtzii</i>	+ .45
<i>A. tetragona</i>	+ .49

The same values of significance apply here, and the remaining two species did not show a significant correlation. One further species, *Enneagonum hyalinum*, also appeared to be an indicator of Gulf water, but was present in too small numbers to be of value. Its occurrence in relation to type of water is shown below.

TABLE III

% Gulf water	0—20	20—40	40—60	60—80	80—100
Occurrence of	— —	—	—	—	— — — — —
<i>E. hyalinum</i>		++	+++	+	+++++

Regression equations indicated that the change in numbers due to water mass was, with one exception, only 15 - 45% of the change in concentration of Gulf water, and so relatively small in comparison

with the large seasonal fluctuations. *E. spiralis*, however, appeared to be mainly a Yucatan water form. An attempt was made to apply a correction for water mass effect to the observed seasonal curves for numbers, but in no case was a significant shift in the peaks produced. It is felt, therefore, that the observed peaks represent genuine seasonal

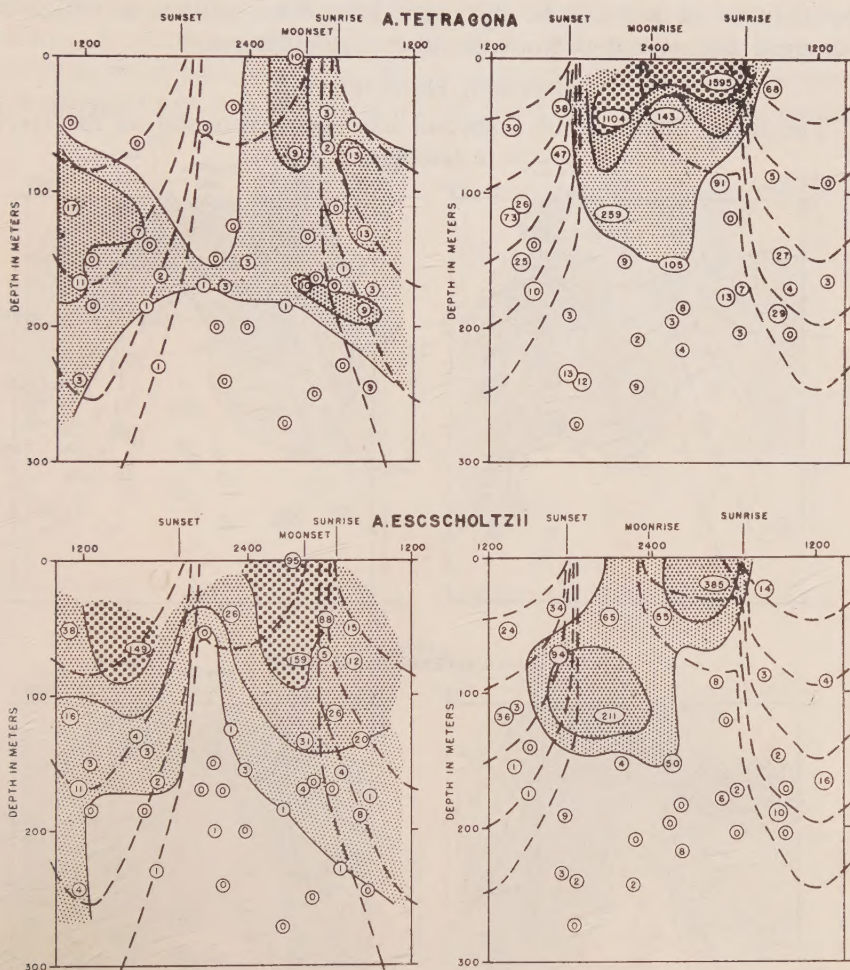


Figure 4.

FIGURES 4-7. Diurnal migration. Numbers represent catch scaled to a standard tow of one mile. The superimposed isolines, reading from the top, represent illumination values of 10^0 , 10^{-2} , 10^{-4} , etc., based on an arbitrary value of 10^2 for surface light with the sun direct overhead.

changes in abundance of the species, and that even the subsidiary fluctuations are likely to be due to some cause other than the changes in proportions of Gulf and Yucatan waters.

The occurrence of a third water mass on two occasions has already been referred to. Since its siphonophore population showed no striking peculiarities, it will not be discussed here. The stations at which it occurred were omitted from the above calculations.

VERTICAL DISTRIBUTION

The mean day level of a species has been expressed as the level

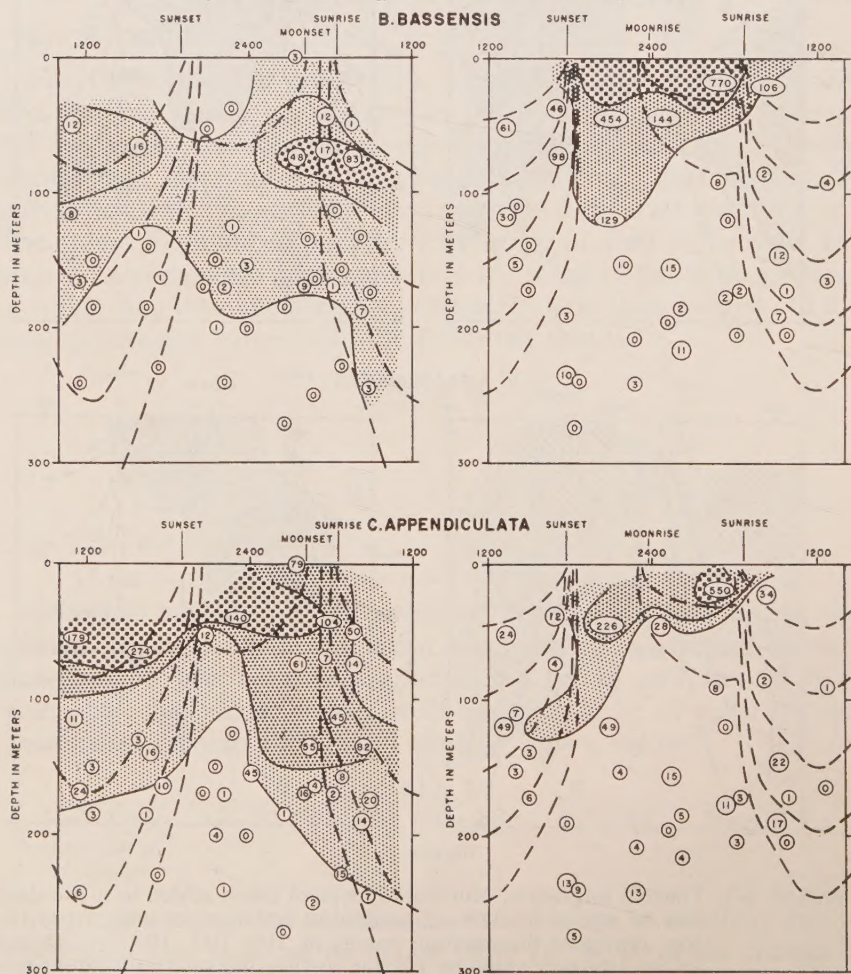


Figure 5.

above which 50% of the population occurs. The over-all mean for the whole period has been arrived at by two methods. In the first method, the mean day level has been calculated for each station at which a sufficient series of hauls was made, and in which the species was sufficiently represented. The over-all value was then obtained as the mean of these various station values. This appears to be the better method. A second method was used where the species was present always in small numbers only. Here, all results for the entire period were grouped together, averaged for 50 meter intervals, and the mean

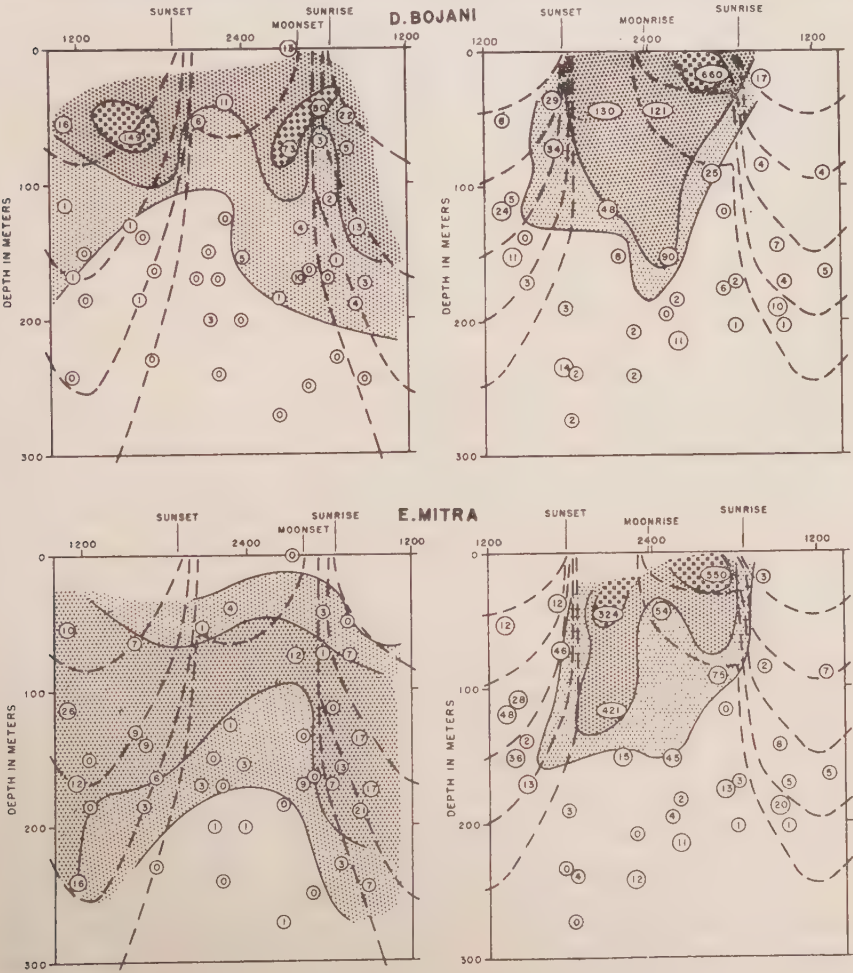


Figure 6.

day level then calculated in the usual way. The second method, because of the nature of these particular hauls, tends to give shallower values and can be taken as little more than an indication of the general level occupied. Table IV shows the values obtained by the two methods, together with Bermuda values for a comparison.

TABLE IV

Species	Mean Day Level—M.			Spread—M.		
	Florida		Bda.	Florida		Bda.
	Method	Method		Method	Method	
	I	II		I	II	
<i>Diphyes bojani</i>	72	29	40	43	88	25
<i>D. dispar</i>	59	40	ca. 10	76	104	10
<i>Eudoxoides spiralis</i>	75	50	65	45	69	65
<i>E. mitra</i>	134	68	125	65	134	105
<i>Chelophyes appendiculata</i>	74	48	75	81	100	130
<i>Lensia cossacki</i>	—	35	—	—	43	—
<i>L. campanella</i>	—	17	60	—	25	25
<i>L. subtilis</i>	—	32	140	—	30	150
<i>L. fowleri</i>	—	100	165	—	102	70
<i>Galettia australis</i>	—	58	—	—	84	—
<i>Abyla leuckartii</i>	—	102	—	—	105	—
<i>Abylopsis eschscholtzii</i>	58	12	ca. 40	51	78	80
<i>A. tetragona</i>	104	85	55	63	122	25
<i>Bassia bassensis</i>	59	13	50	29	75	40
<i>Enneagonum hyalinum</i>	—	100	—	—	28	—
<i>Amphicaryon acaule</i>	—	92	80	—	100	75
<i>Hippopodius hippopus</i>	—	110	140	—	92	75

There is, on the whole, a good agreement between the results from Florida and Bermuda. A detailed comparison must, however, await the availability of data for species from other groups. It is possible, though, to examine the effects of varying water mass on the day level of the siphonophores. The Gulf of Mexico water is, throughout the levels sampled for plankton, about 5°C. colder than the water of the Yucatan channel. Since temperature, as well as illumination, may control the depth of zooplankton, it is to be expected that some species at least will tend to descend deeper during the daytime in the Yucatan water than in the Gulf of Mexico water. In Figure 3, the deviations of level of the various siphonophore species from their overall means for the entire period, are plotted against the depth of the 15°C. isotherm, and it is apparent that the expected adjustment of level to temperature conditions does in fact take place. In fact the regression line indicates that the change in level of the organisms is 95% of the change in level of the 15° isotherm. Studies of additional species will be required before this can be pursued further.

Table IV also shows the Florida and Bermuda values for the spread—that is, the vertical distance between the 25 % and 75 % levels of the species. There is little agreement between the figures for the two regions.

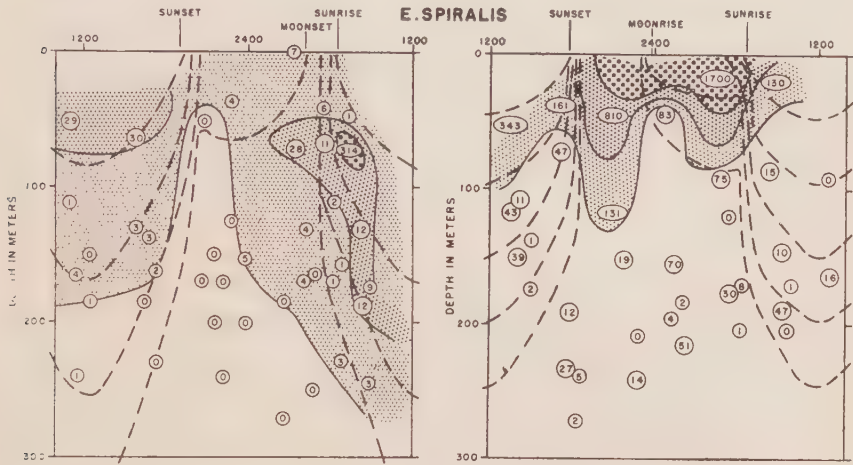


Figure 7.

DIURNAL MIGRATION

Two 24 hour stations were occupied for diurnal migration studies, and the results of these are shown in Figures 4-7. Superimposed on the figures are isolumes calculated for the particular periods which

TABLE V

Species	Day-night range—M.			Day-night ratio		
	Florida		Bda.	Florida		Bda.
	NG.	NG.		NG.	NG.	
	16	32		16	32	
<i>Diphyes bojani</i>	—59	—16	—	18	24	—
<i>D. dispar</i>	—38	+49	—	9	100	—
<i>Eudoxoides spiralis</i>	—33	—30	—	40	93	60
<i>E. mitra</i>	—50	—44	—	12	100	41
<i>Chelophyes appendiculata</i>	—48	—5	—87	29	100	78
<i>Lesia cossack</i>	—	—	—	—	0	—
<i>L. campanella</i>	—	—	—	—	20	—
<i>L. fowleri</i>	—32	—	—	3	21	—
<i>Abyla leuckartii</i>	—92	—	—	6	0	—
<i>Abylopsis eschscholtzii</i>	—6	—48	—	29	28	—
<i>A. tetragona</i>	—70	—80	—89	8	80	61
<i>Bassia bassensis</i>	—28	—41	—	12	100	—
<i>Enneagonum hyalinum</i>	—19	—	—	28	—	—
<i>Amphicaryon acaule</i>	—	—	—77	0	49	83
<i>Hippopodius hippopus</i>	—50	—	—	28	42	—

differed considerably both in the extent of penetration of the light and in the duration of moonlight during the night period. All those species present in sufficient numbers showed some diurnal migration. Values for the day-night range, and day-night ratio are shown in Table V and compared with the available figures from Bermuda. The day-night ratio is an indication of the extent of the night increment into the top 250 meters from deeper water. A value of 100 indicates no increment, while a value of 0 indicates that the whole population retreats below 250 meters in the daytime.

There are too few species for which Bermuda figures are available to allow a useful comparison of the two regions, so this will be deferred until data on other groups is available.

ALTERNATION OF GENERATIONS

In Bermuda, a cyclic alternation of preponderance of the polygastric and the eudoxid generations was observed in several species. In *Bassia bassensis* there were probably five cycles during the year, in *Eudoxoides spiralis*, four, and in *E. mitra*, six. The variation in water mass in the Florida area no doubt complicates the observed pattern, but the three species shown in Figures 8, 9 show at least some measure of cyclic change. *Abylopsis tetragona* is the most clearly defined, with probably five cycles during the year and with good agreement between the two years. *A. eschscholtzii* showed a clear cut peak of eudoxids in the spring and either an extended eudoxid period in the summer and fall, or a period of rapid fluctuation. No definite cycles were observed in this species in the Bermuda material. *Bassia bassensis* showed summer and autumn eudoxid peaks in both years in the Florida material and showed the same at Bermuda. The Bermuda winter peak was, however, missing in Florida, and the two Bermuda spring peaks are represented here by a single extended period, possibly appearing as such on account of too widely spaced sampling. On the whole, though, the agreement between the two regions is surprisingly close. *Diphyes bojani* is included to show the possibility of this species having a double cycle during the year, but the data are too erratic for this to be definite.

DISCUSSION

The purpose of the present survey has been twofold. A survey of the local population of siphonophores, with indications of the seasonal and vertical distribution of the commoner species, has been presented. This survey extended for about a year and a half, and since some of

the characteristics observed in the first year were repeated in the second, it may be assumed that the results are reasonably representa-

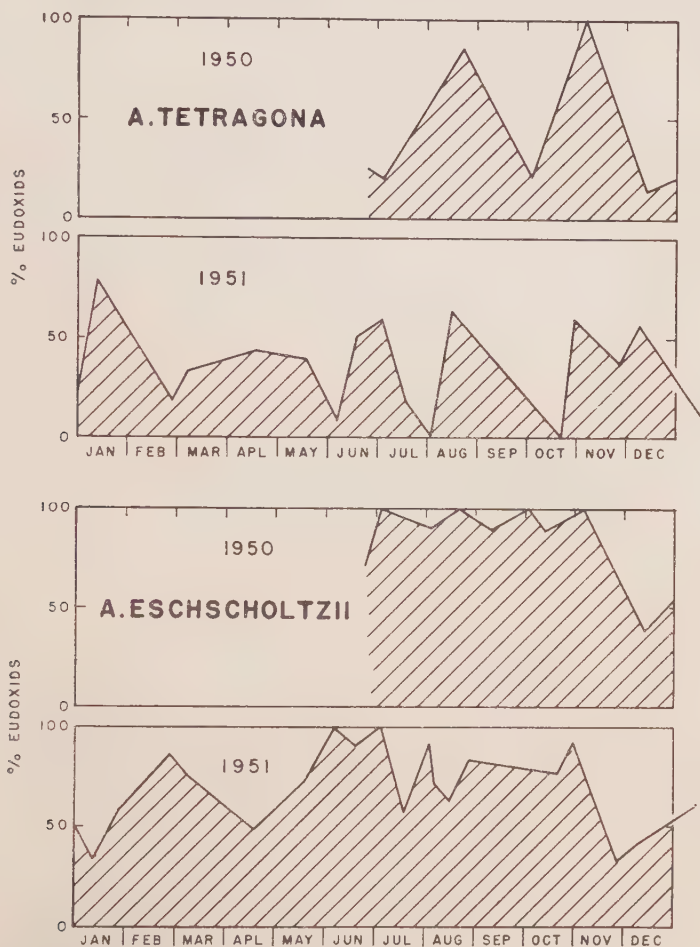


Figure 8.

FIGURES 8, 9. Seasonal changes in percentage of eudoxids present.

tive of typical conditions in the area. Furthermore, the seasonal and vertical distribution of the several species agrees as well as can be expected with similar observations in the Bermuda area, and so lends support to the belief that the results are applicable to a wide area of the western North Atlantic. From the local point of view, it was hoped that some species would be found to be good indicators of the water

masses present in the Miami area, and this has, unfortunately, not proved to be true. Although the abundance of several has been shown to be different in the Yucatan and Gulf of Mexico waters, none are completely restricted to one mass, and so readily useable as indicator species.

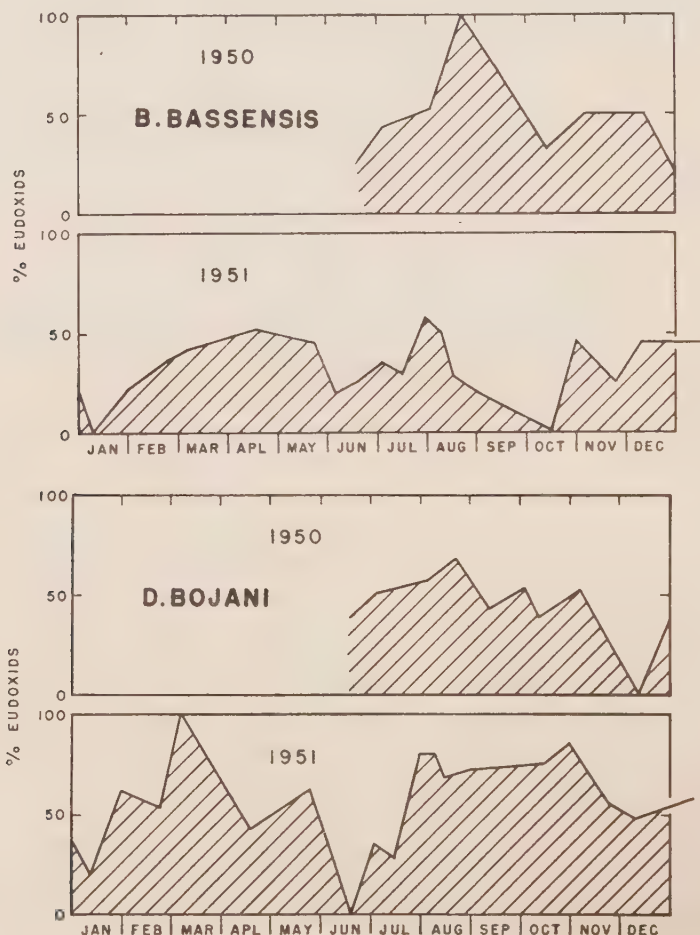


Figure 9.

The second purpose of the survey was a study of the reaction of the plankton species to temporary changes in such conditions as illumination and temperature. This is more readily done when a large number of species can be used for comparison, and will therefore be postponed until results for other groups have been completed. The

only generalization noted here is that among the siphonophores there is a tendency for a change in day level in relation to temperature, the animals moving upward when cold water comes closer to the surface, as it does when there is an influx of Gulf of Mexico water.

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SOME ASPECTS OF THE LARVAL DEVELOPMENT AND METAMORPHOSIS OF *TEREDO (LYRODUS) PEDICELLATA*¹ DE QUATREFAGES²

L. B. ISHAM³ AND J. Q. TIERNEY⁴

ABSTRACT

Since so little is known of the early life history of larviparous shipworms, the larval and early-boring stages of *Teredo (Lyrodus) pedicellata* DeQuatrefages were studied in some detail.

This shipworm, the most common in the Miami area, was cultured in laboratory tanks and used as a source of larvae of a known age.

The anatomy of the larvae was studied and compared, in some respects, with other species of *Teredo*.

The free-swimming and crawling stages were described, as were the early boring stages, in respect to anatomy and behavior. The development of the siphons was described as was the early development of the shells and pallets.

The mortality rate of these stages was discussed.

The speed of swimming and crawling was measured, and descriptive data concerning locomotion were noted.

INTRODUCTION

In spite of the great economic importance of the marine borers (Teredinidae), few studies have been carried out on the larval, post-larval, and early boring stages of this group. The only major report on this subject is that of Sigerfoos (1907), which gives general and detailed information about *Xylotrya gouldi* Bartsch. Hatschek (1880) and others have worked out the early embryology of *Teredo*, but these accounts do not consider larval attachment and boring stages. Sigerfoos's paper, excellent as it is in many respects, does not include any information on the anatomy, development, behaviour, attachment and boring of the larviparous shipworms.

The Marine Laboratory of the University of Miami has, for some time past, been engaged in basic research on marine boring molluscs for the Office of Naval Research. The opportunity was therefore taken to study the larval and postlarval development of the local species, as a necessary preliminary to physiological studies of these stages.

¹The validity of the name *pedicellata*, as applied to the common local shipworm in this and several earlier contributions from the Marine Laboratory, has recently been questioned. In order to clarify the situation, a taxonomic study of the local species is being made, and the questioned name retained for the time being.

²Contribution No. 87 from the Marine Laboratory, University of Miami.

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⁴United States Hydrographic Office, Washington 25, D.C.

METHODS

Cultures were set up in the laboratory to provide a reliable source of *Teredo* larvae for various studies. The cultures were maintained in glass aquarium tanks or in ceramic tanks of a suitable size. Blocks of fir or of pine were placed in the sea nearby for a short period, until a considerable number of shipworms had attacked the timber. The infected timbers were then removed, carefully cleaned and inspected, and placed in the culture tanks. Water entering the tanks was filtered through 120 mesh stainless steel wire cloth, in order to prevent the entrance of planktonic shipworm larvae with the incoming supply of water. Larvae produced in the culture tanks rose immediately to the surface, and were carried by the overflow of water into collecting and concentrating jars. These were similarly provided with 120 mesh filters. The water passed through the mesh, leaving the larvae unharmed in the collecting vessel. The collection jars were inspected every morning and afternoon, and the larvae removed for use by various investigators. The water temperature remained be-

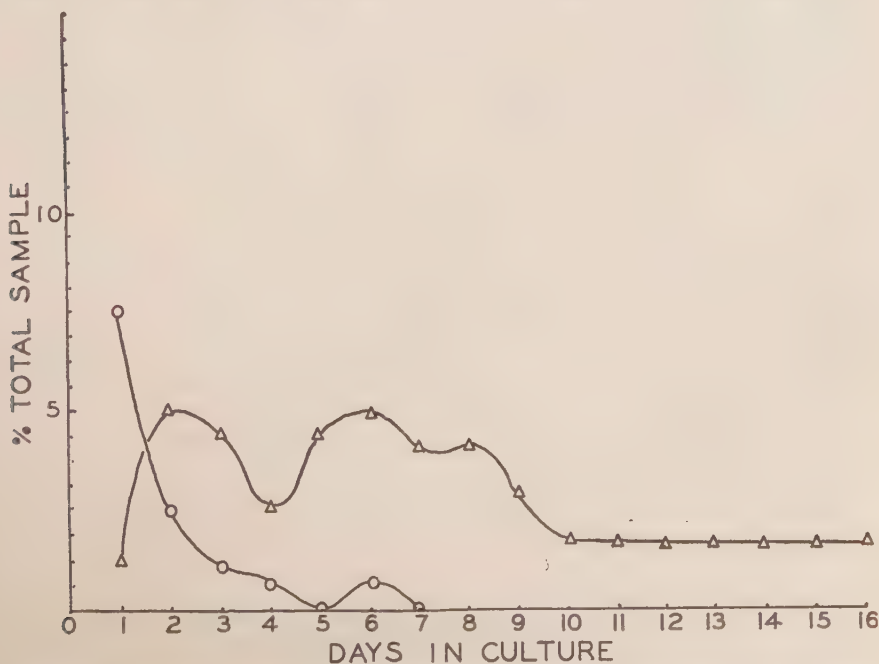


FIGURE 1. Percentages of larvae crawling and boring in cultures in which wood was present. Circles, percentage of larvae crawling; triangles, percentage of larvae boring.

tween 20°C. and 28°C. during the time this study was in progress. The maximum age of the larvae and their history prior to use for experimental purposes was therefore known. Larvae of *Teredo navalis* have been cultured in outdoor tanks, in a similar fashion, in Japan (Imai *et al.*, 1950).

The size of the wooden block is not critical for short term studies on the shipworm. For long term growth studies or for culture work, Dr. Paul Bartsch has recommended that the timbers be no smaller than 4" x 6" x 24", since atypical stenomorphs may be produced as a result of the crowding which occurs in smaller wooden blocks (personal communication).

The most common larviparous marine borer in the Biscayne Bay region, *Teredo (Lyrodus) pedicellata* De Quatrefages, was selected for this study.

The embryos are embedded in the filaments of the parent gill, and there develop to the veliger stage. Release of the larvae is predom-

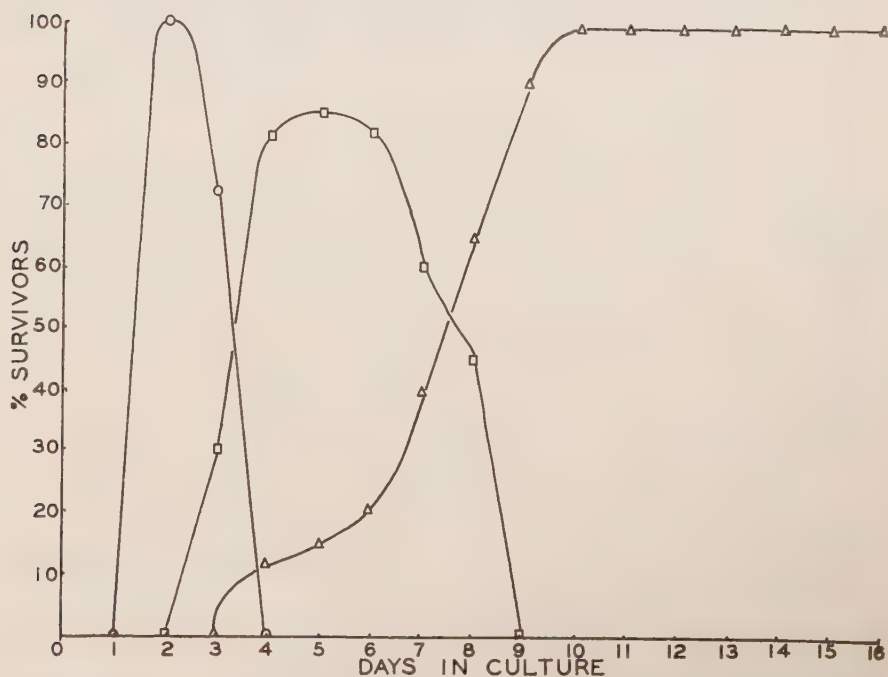


FIGURE 2. Larvae boring into wood. Circles, percentage of borings showing mucoid ring; squares, percentage of borings showing mucoid mound; triangles, percentage of borings showing calcified mound.

inantly a diurnal phenomenon, with the majority of the larvae being released at night. The small, typically pelecypod larvae begin active swimming with the velum immediately following release from the excurrent siphon of the parent.

It has been determined, indirectly, that an entire brood of larvae is not released at one time, but that the liberation of the larvae from the adult occurs over a period of several days. This follows from comparisons between the large numbers of larvae observed in the adult shipworm and small numbers of larvae delivered daily into the filter jars over a period of days. Small catches of five to twenty larvae are as common as larger catches. The greatest number of larvae collected in any 24-hour period was 3,000. From records of the larvae collected from the culture tank, it has become apparent that release of larvae occurs over a period of six to nine days, the average length of this period being eight days. Furthermore, even when numerous adult shipworms are present in the tank, there is a pronounced periodicity in the rate of larval release. During each period of release the rate rises to two maxima, two to three days apart. Of eleven observations, in which the number of larvae released was large enough to demonstrate this, about 60% of the cases showed the first peak to be the greater, while in 40% of the observations the second peak was the greater. These were catches which included 500 or more larvae.

ANATOMY OF THE LARVA

The bivalve shell of the newly spawned larva is globular with an average diameter of 245 ± 20 microns, and entirely contains the contracted soft parts of the larva. The frontal diameter is equal to, or slightly less than the antero-posterior diameter of the shell. Sullivan (1948) reports that the young larvae of *Teredo navalis* measure 80×95 microns, and they settle when 250×220 microns, figures which are only slightly greater than measurements taken from the same species at Woods Hole (Grave, 1928), and in Japan (Imai *et al.*, 1950). Late larvae of *Teredo norvegica*, an oviparous species, are considerably larger, measuring 380 microns in length (Lebour, 1938).

The gape is vertical and the edges of the shell forming the gape are sigmoid. The hinge is a chord of the shell diameter. While early veligers of *Teredo navalis* are straight-hinged (Imai *et al.*, 1950), straight-hinged larvae were never observed in this investigation. The shells have definite umbones, but no teeth or ridges were observed

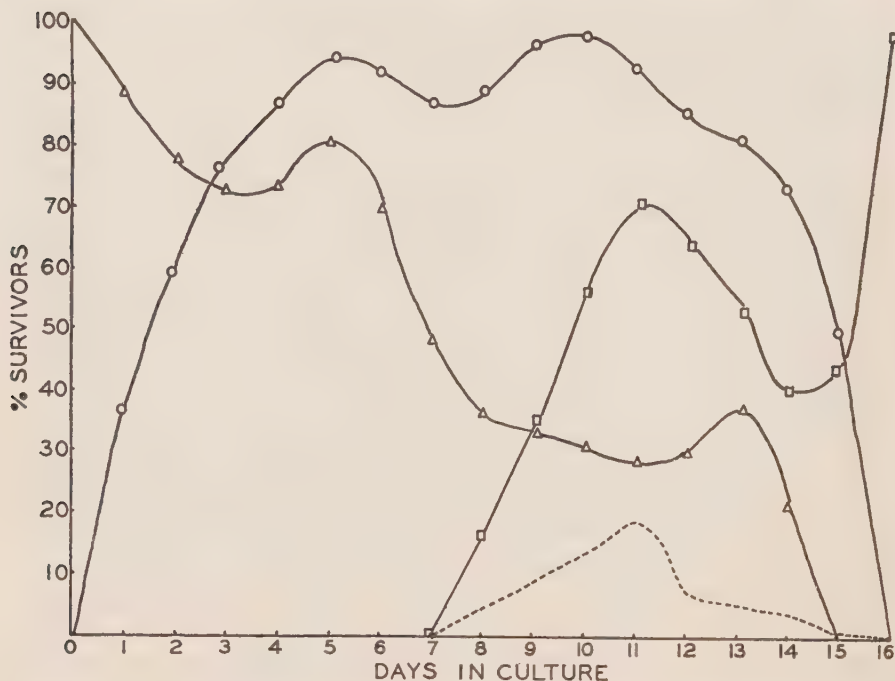


FIGURE 3. Larvae cultured in the absence of wood. Circles, percentage of larvae crawling; squares, mortality rate; triangles, percentage of larvae swimming; broken line, percentage of young showing foot metamorphosis:

until at least 24 hours after release (Figs. 5-7). The larval shell is cuticular in composition and light purplish-brown in color. No evidence of calcareous components was observed until several hours after the young *Teredo* had begun excavations in wood.

The velum of the free-swimming larva is stalked and definitely muscular. When expanded the centrally located stalk of the velum projects above the mid-dorsal portion of the shell. The velum itself is circular, about 245 ± 20 microns in diameter, proportionately smaller than in late larvae of some other species (Lebour, 1938). When fully expanded, its surface may be either plane or slightly concave. There is a definite ciliary pattern on the exposed surface, with a central apical tuft of cilia that are approximately 250 microns long. The activity of the velar cilia is integrated and is wavelike in character, but the rate of ciliary beat is not constant. Attempts to study the rate and magnitude of ciliary action with a stroboscope have dem-

onstrated only that the direction of the power stroke may be reversed, and that the rate is variable within rather wide limits.

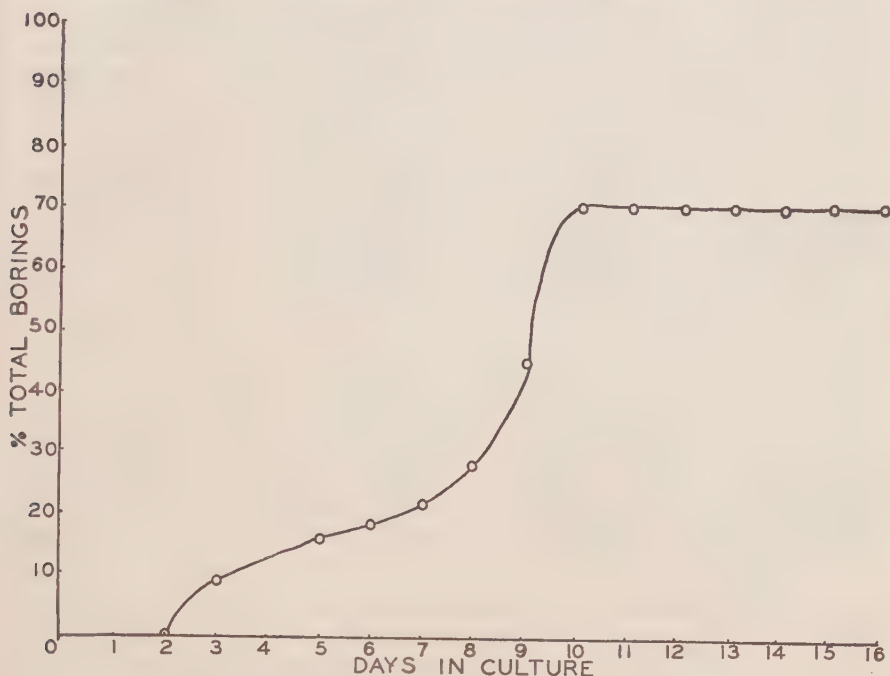


FIGURE 4. Mortality of attached larvae.

The long, narrow, muscular foot is attached by a constricted muscular stalk to the mid-ventral region of the larva. When expanded, it has an average length of approximately 295 ± 25 microns, and an average diameter of approximately 40 ± 6 microns. It is keel-like, and the vertical dimension is approximately twice the lateral dimension. The distal end is slightly expanded and is therefore larger than the stalked proximal portion. The entire foot is muscular and has a ciliated ectoderm. It is very active in the newly released larvae. This differs considerably from the development in *Teredo navalis* where it has been reported that the foot becomes prominent much later, at about 28 days (Imai *et al.*, 1950).

SWIMMING

Immediately upon release from the excurrent siphon of the parent, the larvae begin active swimming. The velum is the sole swimming

organ, and the shell is not used in any way as a locomotor aid. Typical activity consists in a regular straight line ascent followed by a descent which may be either active or passive. In a shallow container, the larvae swim actively toward the surface until contact is made with the surface film. The velum may then be retracted, causing the larva to sink passively to the bottom of the container. The specific gravity of the larvae is greater than 1.0, so that they are obliged to swim constantly in order to remain off the bottom. Instead of retracting the velum and falling to the bottom the larva may so modify the ciliary beat that the organism remains at the surface, but spins on its vertical axis. In a deeper container the larvae usually swim upward, strike the surface film, and then appear to experience a rapid change of posture which directs them towards the bottom. They swim actively during the descent. Typically they do not strike the bottom, but approach it in a curve and start again toward the surface.

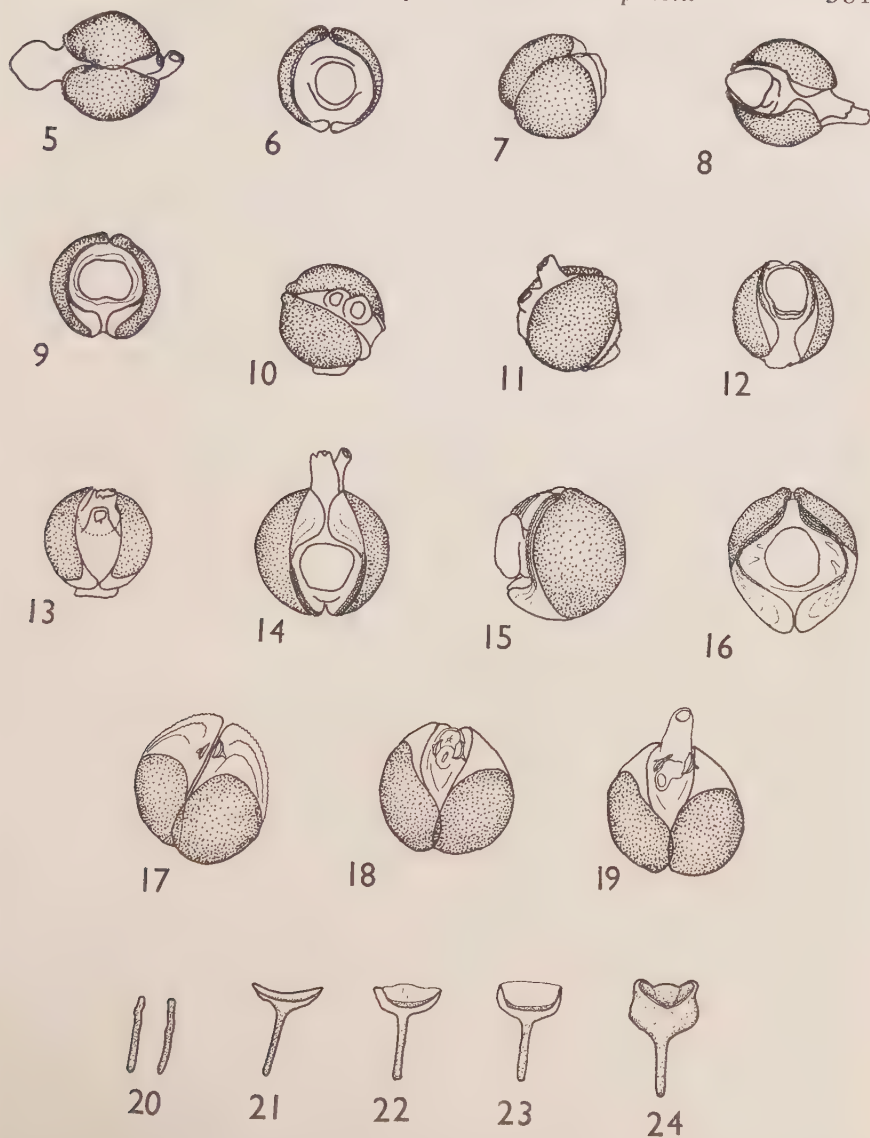
In a tall container the larvae usually do not swim in a straight vertical line, but instead follow a spiral ascending or descending path, retaining their normal orientation with the hinge to one side and the velum uppermost. The foot is frequently extended during swimming. At such times it is always below the equator of the animal and appears to be used as a stabilizer. The velum is capable of considerable flexure. Its angle to the vertical axis appears to control the direction and speed of motion, much as the rotor of a helicopter controls its flight.

The rate of swimming has been determined for larvae that have been free-living for less than 24 hours. Their average rate in a tall cylinder is 7.70 mm. per second upward and 7.01 mm. per second downward, for the straight line portions of their movement.

CRAWLING

The larvae are predominantly swimming organisms during the first 18 - 24 hours after release from the mantle cavity of the adult. If the bottom of the dish or the surface of a block of wood is encountered by the larvae during this period they may crawl on it for a few seconds, but almost at once they resume their swimming activity. As time progresses, however, more and more larvae remain in contact with the bottom or with the surface of the wood. After approximately 24 hours of free-swimming existence the majority of the larvae begin to crawl about on any suitable surface (Fig. 1).

Siphons may be evident about 24 hours after release from the parent shipworm, or they may not develop until just before attachment to



FIGURES 5-7, larvae 12 hours after initial attachment; 8 and 9, 27 hours; 10-12, 36 hours; 13, 60 hours; 14 and 15, 96 hours; 16-19, 132 hours; 20-24, pallets of larvae at 84, 110, 132, 228, and 432 hours, respectively. Figures 5-13, x 50; 14-19, x 65; 20-24, x 200.

the wood; the time of development of the siphons therefore varies within approximately 24 - 48 hours. The siphons appear as small

openings on the mid-dorsal line between the velum and the hinge of the shell (Figs. 10, 11, 13). The newly formed siphons are typically about 24 microns in diameter, and are evidently functional as soon as they are formed. When particulate carbon (India ink) is added to water containing a larva with newly formed siphons, it is very clearly shown that the incurrent siphon is ventral to the excurrent siphon and that a definite flow of water is already passing into the ventral and out of the excurrent siphon apertures. The incurrent siphon is characterized by the appearance of regular peristaltic waves which begin at the ostium and progress toward the base of the siphon, evidently exerting a milking action on the water contained in the siphon.

Although the larvae with siphons are becoming altered into crawling (or boring) organisms, they can still swim with the velum, and can extend the velum, foot, and siphons simultaneously. These older larvae crawl by alternate extension and contraction of the foot, instead of by simple ciliary gliding motions of the type employed by the younger larvae. The foot of the older larva functions in such a fashion that one is reminded of the locomotion of the larvae of the geometrid Lepidoptera. The shipworm larva rests on the bottom, extends its foot maximally, applies the distal tip of the foot to the substratum, and then contracts the foot in a rather sudden manner, flexing it vertically at the same time. The shell is dragged rapidly across the bottom to the attached tip of the foot, the foot is again extended and the procedure is repeated. The larva therefore advances in rapidly repeated, short, forward movements. As the foot is extended, it apparently is used as a tactile organ to examine the texture of the bottom. The foot has, on numerous occasions, been observed to explore the surface of wood blocks, the tip probing into resin ducts and other surface irregularities. This exploratory action by the foot and the jerky motion due to the rapid contraction of the extended foot, results in a lurching, forward motion in a succession of apparently random directions.

The speed and direction of crawling has been determined for a group of larvae 48 hours after release from the parent. A quadrille-lined chart, calibrated with an ocular micrometer grid, was used to plot the movement of each larva. The track of the larva was measured, and temperature and elapsed time were recorded. This random motion (at an average temperature of 25.3°C.) took place at an average speed of 4.821 mm. per minute, or approximately 0.3 M. per hour. This is a not inconsiderable rate of speed, if one realizes that the entire

organism is approximately 245 microns in length. The distal portion of the foot was employed, at every "step," in investigating the surface of the wooden panel.

INITIAL BURROWING

When a suitable site for attachment is found during the course of exploratory crawling, the larva begins to burrow. The boring is usually initiated on spring wood, between the dark, hard rings or lines of summer wood, and is frequently in open resin ducts, small cracks, or other surface irregularities. It is not unusual for a larva to pause in a location, inspect the surface carefully, then move on to another site.

Vital staining of the larvae with dilute neutral red causes a dense coloring of two bilaterally located, glandular regions on the ventral surface of the proximal portion of the foot. Although a byssus has not been observed in this species, these regions may be analogous to the byssus gland of other bivalve larvae, for they aid, evidently by a mucoid secretion, in the temporary attachment of the larva to the burrow site. The larva attaches itself to the surface, rather, the proximal portion of the foot remains relatively motionless, and the distal portion begins to clear away and remove the debris and surface slime from a circular region just in front of the larva. Soft and poorly attached wood cells are also abraded away by the simple mechanical action of the constantly active, distal portion of the foot. It has been noted that no attack takes place on newly exposed panels. The surface of the wood must become waterlogged and the outermost wood cells or fibers must have become more or less dissociated before the larvae can successfully bore into the wood. It is suggested that either the effects of the surface microflora or of the seawater itself, or a combination of both, is responsible for the softening and partial removal of the intercellular material of the wood.

The larva moves forward into the shallow depression prepared by the removal of the surface wood fibers, and begins to enlarge and deepen the hole by the simple mechanical action of the shells. At the time of attachment, or slightly before, minute chitinous teeth form on the ventral edges of the shells. Penetration of the wood takes place with the larva attached by the proximal portion of the foot, the distal end of the foot remaining free and active. Although the larva is firmly attached, in the sense that considerable force is required to dislodge it, the orientation of the larva about the point of attachment is shifted

rather frequently as boring progresses.

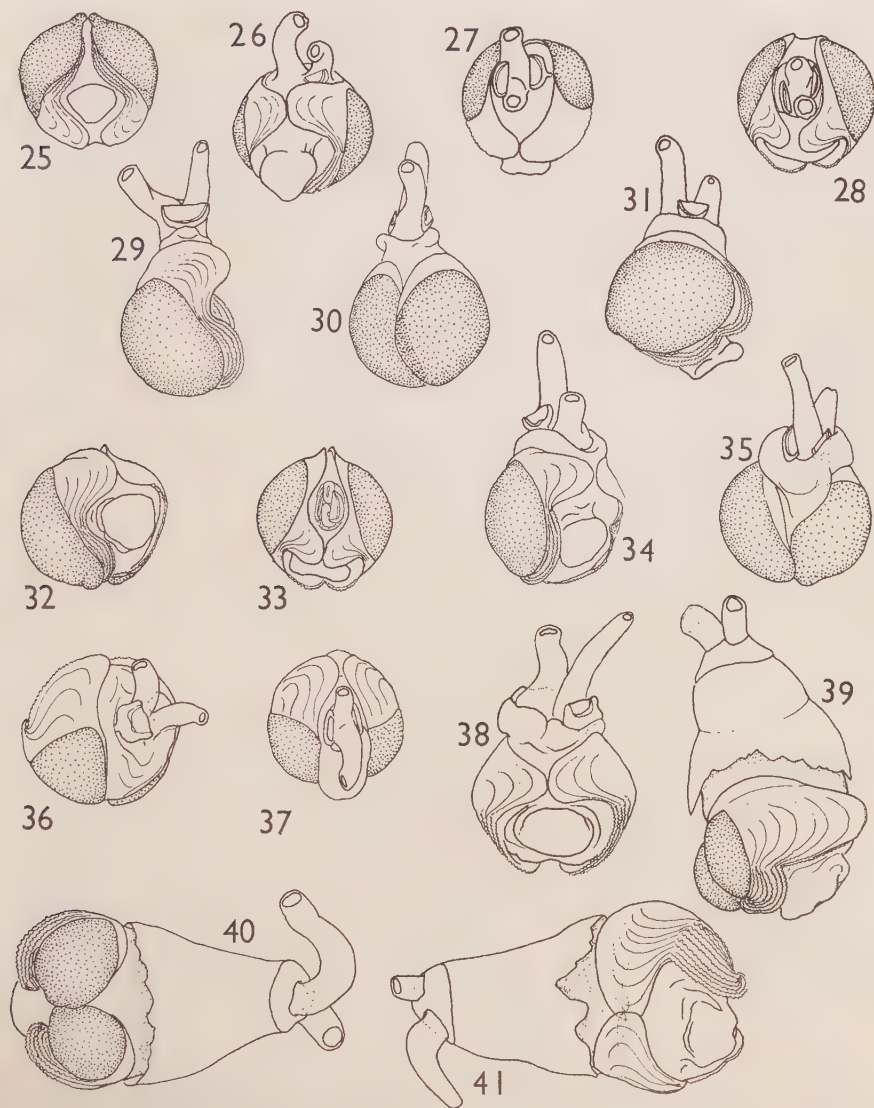
The early excavations are accomplished by the lateral excursions of the shell. The basal portion of the foot holds the shell lip in contact with the wood, and the entire shell is moved laterally. After a movement of approximately 60 microns, the valve in contact with the substrate is elevated, the other valve is lowered, and the procedure is repeated. The shell is also opened and closed in a slow, rhythmic fashion. Shell motions are probably incidental to the movements of the foot in the earlier stages of penetration, although activity of the adductor muscle of the shell undoubtedly plays the major role in the older shipworm as the shell develops teeth and becomes calcified, and thus a more efficient wood-rasping tool.

The activity of the foot at this time is unceasing; the distal end is projected into and over all surfaces of the depression. It frequently functions as a grooming organ, passing over each of the valves of the shell. Infrequently, it can be observed engaged in the same function on the inside of the shell.

In a larva that has produced a slight pit in the wood, after boring about twelve hours, the foot becomes shortened and clavate (Fig. 5). It can still be used to crawl about slowly and it is ciliated distally. After 24 hours in wood, the foot is distally flattened, peltate (Figs. 8, 9, 12), and is frequently observed rotating about its axis, which tends to turn the larva in the burrow, re-orienting the shells in boring. The foot is still quite active, withdrawing or protruding from the shell, but it is not prehensile as in earlier stages. The foot retains this shape, sometimes appearing terminally rounded, but usually flattened, and it protrudes from the shells only slightly in later stages (Figs. 26, 27). There is practically no further apparent change in the form of the foot after 24-30 hours in wood.

As the larva begins boring a slight pit in the wood surface, a ring of debris and mucous soon surrounds the burrow at the surface (Fig. 2). Within 48 hours after settling, all the larvae which begin boring show this ring, which by the fifth or sixth day becomes a mound covering the larva and burrow. Some of the rings or mounds begin to show calcification by the fourth day, and by the tenth day, all burrows are covered by rounded calcareous caps (Fig. 2), continuous with the calcareous burrow lining (Fig. 39).

The siphons, which develop shortly before the animal attaches to wood, extend upward beyond the surface of the wood. The forming, mucoid cap is laid down around them, and two foramina are left



FIGURES 25-27, larvae 156 hours after initial attachment; 28-30, 228 hours; 31-33, 276 hours; 34 and 35, 324 hours; 36-38, 396 hours; 39, 432 hours; 40 and 41, 492 hours. Figures 25-37, x 50; 38-41, x 65.

in the otherwise complete cap. As the embedded shipworm penetrates deeper into the wood, the siphons elongate and increase in diameter.

By the time the larvae have been embedded for 24 hours, the siphons are approximately 60 microns in diameter.

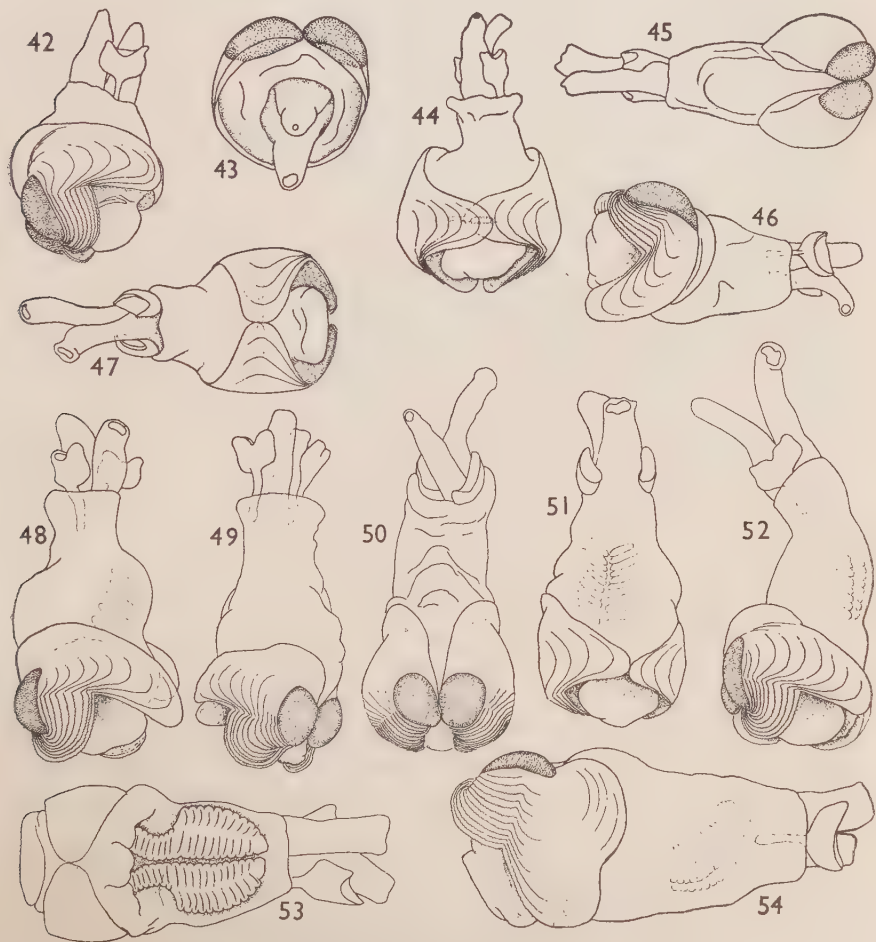
When kept in culture without wood, the larvae exhibit a change in manner of locomotion in that they gradually change from free-swimming to crawling organisms. This change usually takes place within fifteen days after release. In the absence of wood, the larvae are usually dead by the sixteenth day (Fig. 3). As shown in Fig. 3, after one week has passed more than 50% of the larvae have ceased swimming, and depend on crawling for locomotion. At this time, the larvae begin to die and this mortality rate rises sharply from the seventh to the eleventh day, decreases slightly to the fourteenth day, and then rises sharply again to 100% mortality on the sixteenth day. The change from swimming to crawling remains a gradual one with some of the larvae still swimming on the fourteenth day after release. The increase in crawling is greatest during the first five days. The metamorphosis of the foot, in larvae cultured without wood, begins between the seventh and eighth days after release, and the percentage of larvae showing this metamorphosis increases gradually until the eleventh day. There is a gradual decrease in numbers of larvae showing foot metamorphosis thereafter (Fig. 3).

In sharp contrast to the behavior of larvae cultured without wood (Fig. 3), larvae cultured in the presence of wood show a decrease in crawling from the first day onward (Fig. 1), whereas in the absence of wood there is a striking increase in the numbers crawling, from release to the fifth day, at which point over 90% are crawling (Fig. 3). In both cases mortality is great between the seventh and tenth days (Figs. 1, 3). When cultured in the presence of wood the mortality rate reaches a maximum on the tenth day. Under laboratory conditions the mortality rate reached 70% of the total sample of young borings (Fig. 4).

METAMORPHOSIS

The pallets first become apparent as slender, transparent rods (Fig. 20) about 84 hours after boring begins. At 110 hours, the pallets bear a crescent-shaped, distal expansion which is the beginning of the paddle-shaped structure found in adults (Fig. 21). At 156 hours, the pallets are shovel-shaped, with a thickened, crescent-shaped inner margin (Fig. 22) and a slightly concave outer margin. The pallets are slightly concave on the inner side, fitting around the siphons (Figs.

35-37). The concavity of the pallet tips lessens (Fig. 23), but the extremities of the heavy, curved, lower margin grow outward as pointed projections, so that the pallet has a forked appearance. Material is added to this margin, producing a double layer of calcareous material with a hollow portion, this being noticeable at about 432 hours (Fig. 24). At this time the expanded tips of the pallets are quite heavy and opaque, while the stalk is still very slender and trans-



FIGURES 42-44, shipworms 564 hours after initial attachment; 45-47, 612 hours; 48 and 49, 660 hours; 50-52, 828 hours; 53 and 54, 900 hours. Figures 42-47, x 40; 48-54, x 33.

parent. Posner (1951) states that the pallet is three-layered proximally and two-layered distally. The outer layer disappears in the area of attachment of the adductor muscle. There is little further change in the pallet as growth continues. The pallet, growing both in length and breadth, retains its shape and proportions throughout adult life. At some period after six weeks of boring, many specimens of *Teredo* (*Lyrodus*) *pedicellata* have a cuticular layer covering the expanded portion of the pallet, so that the forked pallet tips are brown in color.

After some twelve hours of boring, there is a noticeable addition of calcareous material to the larval shell. At this stage there is one anterior row of teeth and a visible addition to the antero-ventral border (Figs. 5, 7). This is more readily apparent after 36-60 hours in wood (Figs. 11-13). After 60 hours, the rapid shell growth at the antero-ventral border produces an angle where this region adjoins the closely spaced, slowly growing tooth rows of the antero-dorsal portion (Figs. 14-16). This produces an opening for the foot, and at the opposite side, for the siphons (Figs. 17-19, 30, 31, 43). Shell growth continues in this asymmetrical fashion, and about 200 hours after initial boring the body has elongated sufficiently to protrude from the valves. As this condition becomes apparent, the rapidly growing antero-ventral border of the shell produces a slight outward curve where the mantle protrudes (Figs. 29, 32-34). The rows of teeth have, by this time, become numerous (Fig. 25). At approximately 300 hours, the burrow is slightly elongated and acquires a calcareous lining, quite heavy distally but thin and fragile toward the end of the burrow where boring is going on (Fig. 39).

About the same time, the ventral pivotal knob becomes easily visible through the transparent ventral shell border (Fig. 41). The larval shell, cuticular in nature, is still easily distinguished from the calcareous material, and it persists in a recognizable form until the shipworm is quite large. The tooth rows, growing in number and length, are crowded in the median and extreme anterior regions, producing the curving outline characteristic of the adult shell (Figs. 28, 38, 42, 44).

While continued growth produces further elongation of the body and general enlargement of the shell and pallets, there is but little change in the proportions of these parts (Figs. 45-54). With elongation of the body, the gill becomes visible (Fig. 53) as a series of striations seen through the body wall. The gill mass in the young shipworm tapers and curves upward distally (Fig. 54). Beyond this

stage, growth produces little change in form and is largely a matter of body elongation and additional mass of shell and pallets.

Grave (1928) reports that *Teredo navalis*, in some cases, is sexually mature six to eight weeks after entering wood. The youngest specimens, at six weeks, measured 38 mm. at spawning. The same species in Japan was found to be spawning about 65 days after burrowing, at a length of approximately 50.5 mm. (Imai *et al.*, 1950). In the case of *Teredo* (*Lyrodus*) *pedicellata*, panels exposed during all months of the year showed sexually mature shipworms ranging in length from 30 mm. in January, to 75 mm. in July. Over a one-year period, the average figures for sexually mature shipworms was 60 mm. in length, with an average dry weight of 0.0832 gm., exclusive of the calcareous burrow lining. Much larger figures probably would have been obtained had not the exposure period been limited to four months.

In experimental work for previous investigations (unpublished), several successive generations of shipworms were reared under laboratory conditions. It was found that when using test panels of a reduced size, sexually mature shipworms were produced which were extremely small. The test pieces measured only 2" x 1/2" x 1/8", the entire culture procedure taking place in a small, enameled developing tray with running seawater. While the adult shipworms produced are atypical, for study of the early stages the procedure has the advantages of lack of fouling and ease of microscopic examination.

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MARINE FUNGI IN BISCAYNE BAY, FLORIDA¹

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ABSTRACT

A recent collection in Biscayne Bay, Florida, of various marine fungal forms, several previously unreported, indicates the regular occurrence of marine fungi in warmer ocean waters. Two morphologically different forms of such fungi are established, and one form, the genus *Halophiobolus*, is separated into four apparently dissimilar groups to facilitate further species differentiation. Studies reveal the presence of these fungi over a wide marine area, with variation in abundance and types at different localities.

The consistent isolation of these fungi from submerged wood as well as their relative rapidity in the invasion of such wood, suggests an economic role in the primary microfloral complex on wood surfaces in sea water heretofore given minor consideration. Such fungi are apparently primary invaders of wood, and as such, merit further investigation in relation to the deterioration of wood and cordage in saline habitats.

INTRODUCTION

The occurrence of fungi in the microfloral complex of marine habitats and their relation to plant products and remains, other than algae, received scant attention prior to the work of Barghoorn and Linder (1944). Several marine forms of fungi had been reported occurring on algae, but the only marine fungi found prior to 1944 on phanerogamic plant remains were three species of *Ophiobolus*. The investigation by Barghoorn and Linder, primarily concerned with the New England area, revealed many previously unreported marine fungi on wood and cordage submerged for long periods in marine habitats. Laboratory cultures of several species of these fungi exhibited consistently more rapid development at higher temperatures, and their greater destructive action on wood and cordage in warm or tropical waters than in cooler northern marine areas was suggested. No extensive study has been made of marine fungi in tropical waters, and with the exception of a footnote in the above-mentioned paper merely noting the occurrence of the perfect and imperfect stages of different species of marine fungi from Biscayne Bay, Florida, no investigation has been made of the marine fungal flora of this area.

The current introductory survey notes the occurrence and describes the predominant marine fungi collected in a six-month study of test panels submerged at various localities in Biscayne Bay, Florida. In addition, some indication is given of their possible economic role in

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the deterioration of wood and cordage in marine waters. Barghoorn and Linder (1944) have stated that certain marine fungi are instrumental in speeding the decay of wooden pilings and particularly cordage by the successive and continuous erosion of the submerged outer surfaces. This important problem is currently under investigation with the marine fungi collected during this survey, and will be discussed in a later publication.

All of the fungi described in this paper are true marine forms, and several fungi, collected infrequently or usually terrestrial in origin, have been omitted. Among such fungi are those characterized by reproductive structures found on wood immersed for long periods of time and morphologically different from those described below. If these forms are found to be normal marine inhabitants, their description and occurrence will be reported. Several of the fungi described here have not been reported previously and appear to be new fungal types, while others, in the genus *Halophiobolus*, have been found further south than has been reported previously.

The writer wishes to express his sincere appreciation to Dr. E. S. Reynolds of the Marine Laboratory, University of Miami, for his counsel and guidance during the entire course of this study, and to J. B. Lewis of the Marine Laboratory for his assistance in the preparation of the photomicrographs.

METHODS

The marine fungi reported in this paper were collected by exposing in the sea water, yellow pine panels, $\frac{3}{4}$ x 5 x 6 inches in size. These were fastened in pairs to bronze sashweight chain cut into lengths of 8 to 12 feet, corresponding to the water depth at each station. The chain was anchored to the bottom with cement blocks, while the upper portion was secured to pilings, docks or buoys. In addition to these test panels, numerous collections were made from pilings and driftwood throughout the bay.

This arrangement of the test panels allowed for optimum study of the marine fungal forms attached to the inner surface of the panels. The rapid coverage of the outer panel surface by microscopic fouling organisms voided the use of these surfaces in the study. The panels were submerged continually from 6 to 22 weeks, varying at different stations, and removed for microscopic examination, beginning after 4½ weeks exposure. Following examination, the panels were disposed of, and new, unexposed panels were replaced at the various stations.

This procedure enabled the study of newly submerged panels, as well as older ones, throughout the exposure period, and also permitted the observation of any seasonal effect on fungal distribution.

The stations at which panels were submerged were established with reference to the ecological study of the Biscayne Bay area by Smith *et al.* (1950), and the location of abandoned and decayed wharfs, pilings, cordage and driftwood. The Fisher Island station (No. 1) is an area of abundant old wharfs and pilings and receives a continuous tidal flow through Government Cut. The Flamingo Hotel docks station (No. 2), Beach Boat Slips station (No. 3) and Marker 22 (No. 4) were considered representative of the northern bay where moderate amounts of sewage occur. The station at Marker #16 (No. 5) is adjacent to the Miami dock area, receiving considerable sewage outflow, while the Marker #14 station (No. 6) is near the mouth of the Miami River. A station (No. 7) was established at the Florida East Coast Railroad bridge, well within the Miami River area. The station at the southwest tip of Virginia Key (No. 8) is far from the mainland and receives less sewage flow.

It was necessary to establish a basis for the collection and examination of material to insure that the fungi isolated are normally marine in occurrence. The panels were submerged continually throughout their entire test period and examined one to two days following removal from the bay. Wood samples, either continuously immersed or located in the intertidal zone and subject to immersion twice a day in salt water, were collected from widely separated bay areas. These revealed a fungal population similar to that collected on the test panels. Additional evidences of the tolerance of these fungi to a marine environment were their vigorous spore germination in sea water as well as fungal growth on artificial media made with sea water.

To facilitate the morphological differentiation of these fungi, two separate groups were established utilizing the main diagnostic features of the spores of the fungi involved. Further separation of these variable forms by cultural methods is necessary to ascertain definite differences between species. The following classifications will be followed throughout this paper. Form 1: ascospores slender, filiform, hyaline, with a gelatinous appendage-like tip at the spore apices. These filamentous spores characterize fungi of the marine genus, *Halophiobolus*, described by Linder (Barghoorn and Linder, 1944). Form 2: ascospores ellipsoid or elongate-ellipsoid, hyaline, 2-celled, with two long, slender, hyaline appendages at each of the spore apices.

DESCRIPTIONS

For recognition of the variable ascocarpic types within this fungal form, the following groups are established, utilizing the main differences in these spore-bearing structures.

FORM 1 (FIGURES 1-12)

Group 1. Ascocarps scattered or occurring in concentrated groups, superficial to partially imbedded (found within fissures in wood surface), globose to ovate, ostiolate, black, carbonaceous, collapsing on drying, apparently variable in size, 249-464 (average about 321) microns long and 185-214 microns wide (long-necked ascocarps of this group isolated from cordage measured 585-699 microns long and 192 microns wide); neck papillate to elongate, central, dark fuscous under microscope, covered by a layer of colorless material, finely striated, 16 microns wide (similar width throughout entire neck length), as long as 350 microns; asci not seen, probably deliquescent early in maturity since ascospores occur in groups of eight; ascospores hyaline, slender and filiform, with a hyaline gelatinous tip at both ends of the spore, variable in length, 320-350 microns long, with those isolated from ascocarps on cordage, 214-307 microns long. (Figures 1, 2).

Group 2. Ascocarps scattered to gregarious, mostly superficial, globose to sub-globose and spheroid, ostiolate, hyaline or sub-hyaline at first, becoming fuscous to dark fuscous on maturity, membranous, variable in size, from a long-necked group, 568-699 x 163-177 microns, to a short-necked group, slightly papillate to 350 microns long and 178-249 microns wide; neck central, slightly extended to greatly elongated, hyaline to light fuscous, occasionally dark fuscous at base of neck, surface rough with striated appearance, often enlarged or apparently deformed at apex, as long as 534 microns, either exerted its entire length beyond the substratum or lying parallel upon the eroded wood surface, approximately 24 microns wide, with some necks slightly wider at the base than at the apex; asci not seen, apparently 8-spored as ascospores occur in groups of eight; ascospores similar to Group 1 in appearance, 343-570 microns long (majority about 450-500 microns long). (Figures 3-6).

Group 3. Ascocarps occurring successively either in a single wood element or in several such neighboring elements, imbedded in the outer wood layer, cylindrical or subcylindrical, ostiolate, dark fuscous to black, appearing fuscous under the microscope, membranous, collapsing on drying, 342-464 microns long and 57-71 microns wide;

neck papillate to elongate, hyaline to light fuscous, apparently darkening with maturity, slightly striated under the microscope, central to terminal, as long as 350 microns in length; asci and ascospores apparently similar to above groups. (Figures 7, 8).

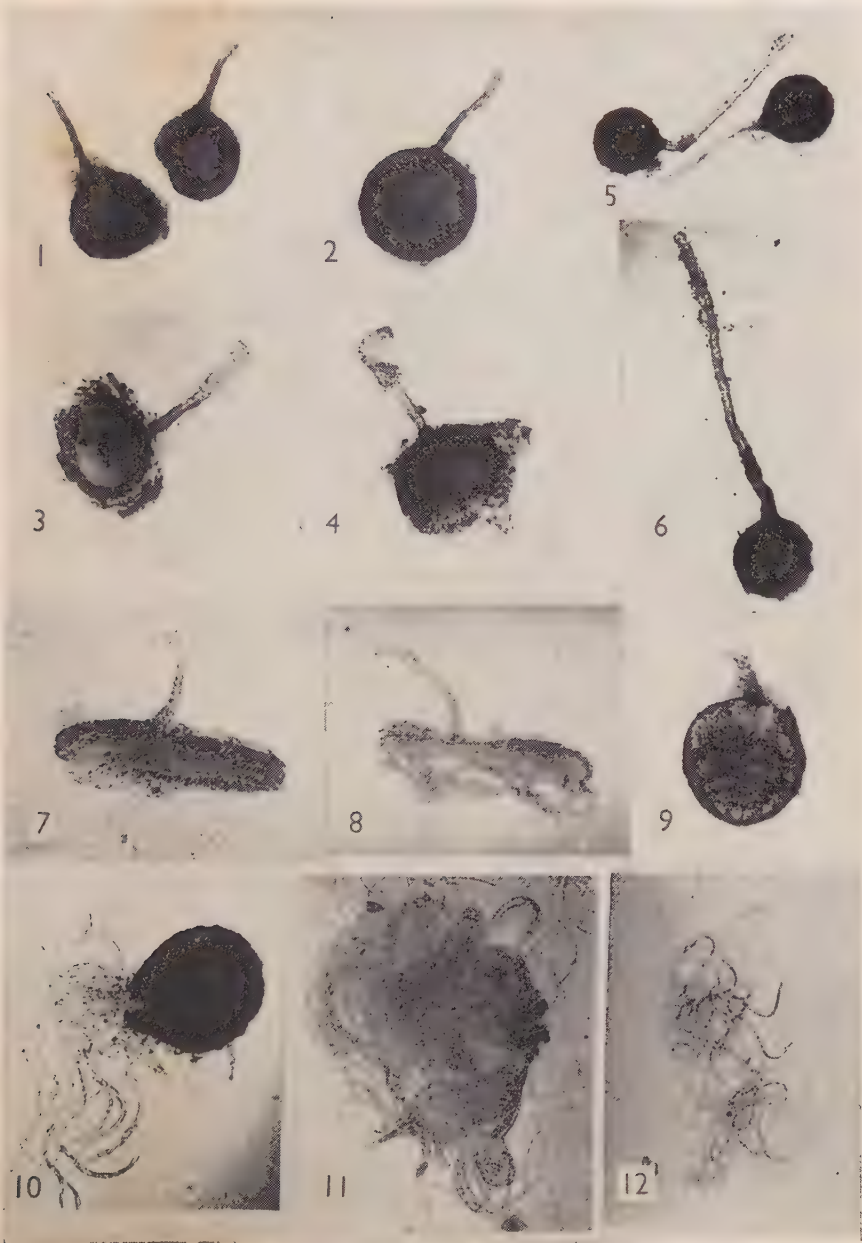
Group 4. Ascocarps scattered, superficial, hyaline at first, later dark fuscous to black, membranous becoming slightly carbonaceous on maturity, surface verrucose, globose to sub-globose (some slightly ovate), non-ostiolate to papillate (mostly cleistothecial-type), 285-392 microns in diameter at maturity; asci elongate-clavate, 8-spored, hyaline, deliquescent later in maturity than above groups; ascospores similar in appearance to above groups, 232-313 microns long (majority 250-285 microns in length). (Figures 9, 10).

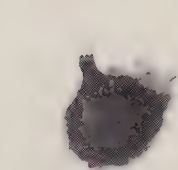
FORM 2 (FIGURES 13-24)

Ascocarps imbedded in wood matrix, becoming exposed by erosion of the decayed wood, solitary or somewhat gregarious, black, carbonaceous, globose to sub-globose, ostiolate, variable in size and shape, 371-514 (majority about 464) microns in length and 249-285 microns wide, with black rhizoid-like hyphae ramifying from the basal portion; neck exerted variable distances beyond substratum, central, light to dark fuscous with hyaline cells at apex, 142-285 (majority, 214) microns in length and 42 microns thick; asci 8-spored, elongate-clavate with rounded apex and a slender tapering stalk, deliquescent at maturity; ascospores ellipsoid or elongate-ellipsoid, hyaline, 2-celled, each containing a single conspicuous globule or several smaller globules, 27-32 x 9-9.8 microns, with two long, slender, flexible, hyaline appendages, approximately 24 microns long, at the spore apices, appendages inserted slightly behind the spore tip, arranged at 90° to those at the opposite end.

FORM 1

- FIGURES 1, 2. Globose ostiolate ascocarps (Group 1) of Form 1, x 60.
 FIGURES 3, 4. Short-necked spheroid ascocarps (Group 2) of Form 1, x 60. Note the hyaline appearance of the neck and the swollen area along the neck apex.
 FIGURES 5, 6. Long-necked ascocarps (Group 2) of Form 1, with smaller globose base. Figure 5, x 60; Figure 6, x 70.
 FIGURES 7, 8. Elongated ascocarps (Group 3) of Form 1. Cylindrical base is entirely imbedded in wood matrix. Figure 7, x 90; Figure 8, x 75.
 FIGURES 9, 10. Cleistothecial-type ascocarps (Group 4) of Form 1, x 65. Figure 10 shows 8-spored asci escaping from ascocarp.
 FIGURE 11. Ascosporic mass, with asci and ascospores from an individual ascocarp, x 65.
 FIGURE 12. Filiform asci and ascospores of Form 1, x 40.





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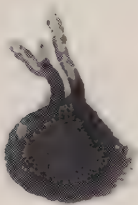
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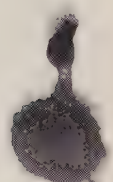
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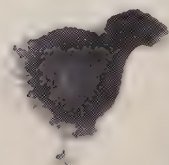
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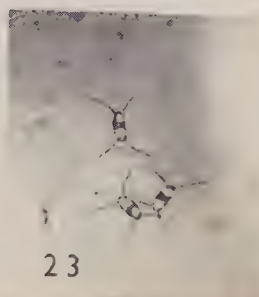
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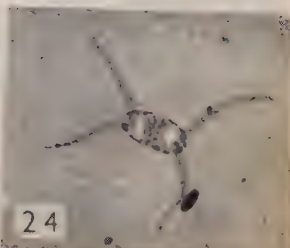
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24

Thus, considerable morphological variation exists between the ascocarps within the two forms, particularly in size, shape and relation of these spore-bearing structures to the wood tissue. While the depth within the wood matrix of the elongate-necked ascocarps (Group 2) of Form 1 appears to influence the length of the exerted neck, superficial ascocarps of this group have as long, if not longer, necks. These necks, under the microscope, appear as hyaline to light fuscous, rhizoid-like structures, lying upon the wood substratum. In addition, the superficial papillate to short-necked ascocarps of this group vary morphologically from one wood area to another. These variations may possibly be attributed in part to the release of available nutrients to the developing fungi by the decomposition of the organisms in the surface growth on the wood. Such an occurrence may explain the more greatly extended and thicker necks of ascocarps observed growing within the relatively nutrient-rich medium of the inner surface of barnacle shells attached to the wood panel.

The elongate-cylindrical central neck is typical of the ascocarps of the Form 2 fungus (Figures 13-15), although exceptions to this structural characteristic are noted. Foremost among these are the bulbous swellings of the neck wall at either the base or apex, often causing a general distortion of the neck area (Figures 18-22). In addition, superficial, large, sub-globose, non-ostiolate to slightly papilliform ascocarps of this form have been isolated from immersed wood at several localities, some having spores with more (3-4) than the usual two hyaline appendages at each end. Another unusual modification of this form is the occurrence of fused ascocarps, as well as single ascocarps having two distinct, well-formed necks (Figures 16, 17). The

FORM 2

FIGURES 13-15. Normal ascocarps of Form 2, exhibiting differences in neck length, $\times 50$. Fungal mycelium and remains of wood matrix adhere to the basal portion of the ascocarpic body.

FIGURES 16, 17. Bi-ostiolate ascocarps of Form 2, $\times 50$. Neck arrangement of ascocarp in Figure 16 apparently caused by fusion of the bulbous base of 2 ascocarps. Necks in Figure 17 arise from one ascocarp base.

FIGURES 18-22. Ascocarps of Form 2, showing variation in neck size and shape, $\times 50$. Figures 18-20 illustrate the bulbous swelling of various portions of the neck wall, while Figures 21-22 show malformations occurring in the general structure of the neck.

FIGURE 23. Bi-appendaged, 2-celled spores of Form 2, showing arrangement of the appendages at the spore apices, $\times$ approx. 150.

FIGURE 24. Form 2 spore enlarged, $\times$ approx. 330. Note insertion of appendages slightly forward of the spore tip and arranged 180° to one another at one end, and 90° to those at the opposite end.

appearance of the hyaline cells at the neck apex also varies greatly, often undergoing a gradual disintegration with increasing maturity of the ascocarp.

The morphological structure of the spores of these fungi indicates an adaptation to a marine environment, both in suitability for aquatic dissemination and ease in surface attachment. The appendage-like processes evident at each end of the spores of Form 2 (Figures 23, 24) serve to keep the spore suspended in water, while the arrangement of the appendages permits more definite movement in an aquatic medium. In addition, they serve to facilitate attachment of the spore to submerged surfaces, as seen by the adherence of these filament-like processes to the cover glass or slide in hanging drop preparations. The spores of the *Halophiobolus* groups (Figures 11, 12) are long and filamentous and thus more readily suspended and disseminated in water. Also, the two ends of the spores are equipped with modified tips, capable of readily attaching the spores to a submerged surface. An additional modification is the dissolution of the ascus wall early in the formation of the ascospores, thus facilitating the release of these spores into the surrounding aquatic environment. It was observed that tendril-like spore masses (cirri) exuded from the ostiole of necked ascocarps following several days of incubation of the infected panels in a moist atmosphere.

OCCURRENCE AND DISTRIBUTION

Examination of the test panels at the various stations following 4½ weeks submergence showed an abundant fungal flora, as indicated by the fruiting structures, occurring in groups and singly over the entire wood area, particularly evident on the inner surface of the panels. This initial colonization, appearing as perithecial-type ascocarps, both superficially on the eroded wood surface and deeply imbedded in the outer matrix of the wood structure, was predominantly, if not entirely, Form 1 (Figures 1-10). Following longer periods of submergence, the incidence of the imbedded type of ascocarp (Groups 1 and 3) of Form 1 increased, causing deep pits in the softened wood surface. This form, abundant on panels submerged 4 to 6 weeks, was only slightly present on the panels submerged 9 weeks, and noticeably absent after 16 weeks submergence. However, one series of panels submerged 13 weeks at the Fisher Island Station showed a large colonization by Group 1 of Form 1.

Form 2, characterized by imbedded perithecial-type ascocarps

(Figures 13-22), was present on panels submerged 9 weeks at Fisher Island, with such fruiting structures increasing in abundance with continued submergence. Panels submerged 22 weeks at Fisher Island revealed a variable population of the Form 2 fungus, differing in concentrations of ascocarps between separate panels. In addition, the dispersion of the ascocarps varied greatly among different areas of the same panel. This positional dissimilarity in the ascocarps on the wood surfaces appears to be due to the differences between panels in regard to the arrangement of the various wood elements. The fungal structures are distributed in lines coincident with the direction of the wood elements, and under higher magnification, appear consecutively along any one wood element. This condition indicates a directional ramification of the fungal mycelium through the wood tissue following infection.

Such variation in the presence of these two fungal forms suggests a possible ecological succession, influenced by length of submergence and condition of wood surface. With the one exception mentioned above, Form 2 succeeded Form 1 as the length of submergence increased, resulting in the dominance of the one form. In the exception to this rule, it was noted that the wood surface was eroded only slightly and bore a minimum attachment of fouling organisms, while usually panels submerged for shorter periods (4½-9 weeks) were completely covered by barnacles and other growth. These latter panels after 9 weeks showed vigorous colonization by Form 2, accompanied by considerable deterioration of the wood surface. It appears that the amount of erosion of the wood, in addition to colonization by marine animal forms, affects the relative abundance of the Form 2 fungus. On panels of equal periods of submergence, Form 2 was more abundant on those surfaces exhibiting greatest deterioration.

Whether this increased wood decay results from activities of the fungus itself is yet to be determined. However, some definite evidence does point to the role of these fungi as primary invaders of submerged wood. The appearance of the fungi on the wood surface prior to the attachment and growth of barnacles and other fouling organisms is evidenced by the imbedding of the fungal ascocarps well beneath the calcareous material deposited by barnacles and other marine animals. Also, enlarged fungal bodies of Form 1 were found growing in a concentric ring at the inner basal portion of individual barnacle shells attached to the wood panel. Other ascocarps of Forms 1 and 2 were equally apparent on the wood surface beneath the surface

growth of various benthonic organisms. The ascocarps of Form 2 have often been isolated from wood beneath the calcareous lining of *Teredo* burrows deep within the wood tissue, as well as found imbedded in the soft pulpy woody tissue of older burrows caused by such marine wood boring organisms. In addition, prepared sections of fungus-infected wood tissue reveal the presence of abundant fungal hyphae penetrating the walls of the wood vessels, as well as ramifying through the bordered pits and at times forming a fungal mantle in the two or three outermost cell layers of the wood.

Both Forms 1 and 2 were found widely distributed over the Biscayne Bay area, with Form 2 being collected on driftwood obtained as far south as Big Pine Key. As mentioned previously, this particular form has been isolated continually from long submerged and decayed pilings and driftwood. Form 1, however, has not been noted on such older and more decayed wood, but has been more apparent on recently immersed material. This condition is similar to that occurring on the test panels where Form 2 gradually succeeded Form 1, with final domination of the former fungus.

The distribution of the Form 1 fungus varied among the stations, being especially abundant at Stations 1 through 6. At these stations, variations occurred in the prevalence of the different groups of Form 1 on individual panels. Group 1 was most abundant at Stations 5 and 6 after 6 weeks submergence, while Groups 2 and 3 were most abundant at Stations 1 through 4 during the same length of exposure. Group 4 of Form 1 was particularly evident on panels at Station 3, and this ascocarpic type noticeably developed in population and size of individual ascocarps upon exposure for several weeks in humid laboratory containers. Group 1 appears to succeed the other groups of Form 1, for while Group 1 was obtained on panels submerged as long as 13 weeks, Groups 2, 3, and 4 were dominant after 4½ weeks exposure, and gradually decreased in abundance with increased submergence.

The Miami River Station revealed a noticeable absence of Form 1, even after 7 weeks submergence, and Station No. 8 at Virginia Key showed a slight amount of Groups 1, 2 and 4, compared with other stations of similar and less exposure time. However, panels at this latter station after 9 weeks exposure exhibited a large population of Group 3, noticeably characterized by being more deeply imbedded in the wood tissues than ascocarps on panels at other stations. The

Form 2 fungus, abundant at Fisher Island, and collected on immersed wood at various Bay localities, has not been noted yet on test panels at any of the other stations.

No correlation between such variable distribution and marine ecological conditions can be established as yet. However, further study of test panels is in progress, both at the above mentioned stations and at newly established ones, to determine the effect of longer submergence periods on the fungal complex and the incidence of other fungal forms.

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A NEW FAMILY, GENUS AND SPECIES OF MYOPSID SQUID FROM THE FLORIDA KEYS.¹

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ABSTRACT

A new genus and species of myopsid squid, *Pickfordiateuthis pulchella*, is described from specimens collected at various stations in the Florida Keys. Because of certain differences, this species is designated as the type of a new family, Pickfordiateuthidae, which appears to be closely related to the Loliginidae. Its habitat, range, and possible relationship to other families of the myopsid squids are discussed.

The specimens described in this paper were collected by Mr. Craig Phillips of the Marine Laboratory of the University of Miami, at several stations in the Florida Keys. They are remarkable in that they belong to a new family of myopsid squids and are the smallest species of this group now known from the Western Atlantic. The present specimens show strong affinities to the Loliginidae but differ from this family in so many respects that it has been considered necessary to form a new family for their proper disposition rather than to broaden the conception of existing families and to inject confusion into the ranks of old and well-established systematic units.

Family PICKFORDIATEUTHIDAE, new family

Body cylindrical, bluntly tapering posteriorly; fins large, round, dorso-laterally inserted, not connected posteriorly, sepiolid-like; eye imperforate, pore minute or absent, eyelids lacking; nuchal cartilaginous locking organ present, mantle not fused to the head; gladius well-developed, feather-like; left oviduct functional; left ventral arm of male hectocotylized; tentacular club with two rows of large suckers, distally with four rows of minute suckers.

Pickfordiateuthis pulchella, new genus and species

Material:

Holotype. One female, preserved in formalin, from three feet of water over grass bed at Old Rhodes Key, Florida, February 3, 1950. Craig Phillips, collector. USNM 574846.

Paratypes. One male, one female preserved in formalin, from under pier at Key West, Florida, November 1949. Craig Phillips, collector. Second University of Miami-Cay Sal Expedition. ML

¹ Contribution No. 89 from the Marine Laboratory, University of Miami.

31.48. One female, preserved in formalin, from Crandon Park, Key Biscayne, Florida, February 1950. Craig Phillips, collector. In author's collection.

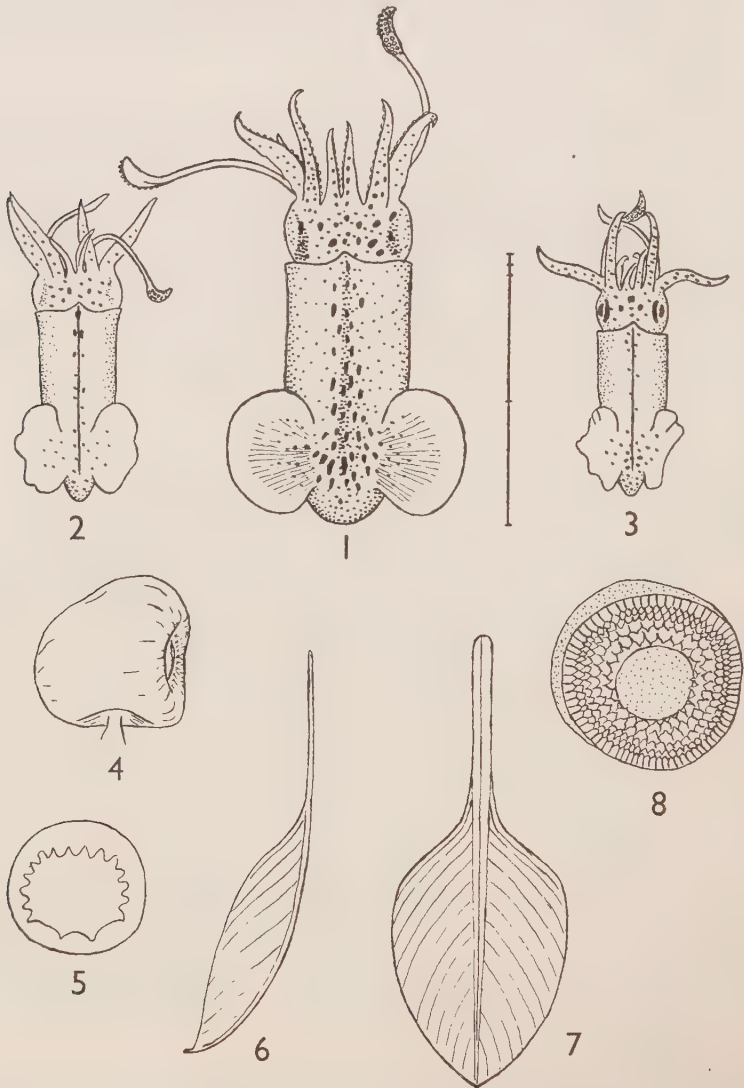
Description. The animal is small, somewhat sepiolid in form (Figs. 1-3). The mantle is cylindrical, slightly swollen near the middle, tapering to a rather blunt point posteriorly, the antero-dorsal margin produced to an acute point on the midline, the antero-ventral margin deeply emarginated beneath the funnel, produced into acute points on either side. The fins are large, round, about one-half the mantle length, dorso-laterally attached anterior to the posterior end of the mantle, sepiolid-like. The head is large, twice as broad as long, wider than the mantle, flattened. The eyes are prominent, without an accessory lid and without a visible pore.

The arms are strong, of moderate length, in the order 3.4.2.1., the third pair much the stoutest and longest with a conspicuous, broad, well-developed swimming membrane. The first pair of arms is very short bearing a conspicuous, broad swimming membrane on the dorsal surface. The second pair is devoid of a swimming membrane. The fourth pair of arms is flattened ventrally, the inner edge bearing a low sharp ridge, the outer edge with a broad membrane within which lie the tentacles. The arm suckers (Fig. 4) are in two rows, barrel-shaped with short pedicels inserted laterally, the rings armed dorsally with small blunt teeth, ventrally with three or four large blunt teeth (Fig. 5). All of the arm suckers are bordered by thin protective membranes with supports.

The tentacles (Fig. 9) are long, stout, rounded dorsally and compressed ventrally, the clubs compact and bordered dorsally by a swimming membrane. The tentacular suckers are in two rows on the club, four rows distally, surrounded by a protective membrane with supports. The sucker discs are equipped with small, even-pointed teeth (Fig. 8); the rings are smooth.

The left ventral arm of the male is hectocotylized (Fig. 16) by the distal fourth of the arm bearing only a single row of suckers, the inner row of suckers being lost and replaced by a heavy pad-like membrane into which the outer row of suckers is partially inserted.

The gladius (Figs. 6, 7) is well-developed, fragile and thin; the rhachis is narrow, highly keeled, with delicate thin borders. The vane is two-thirds of the total length, very broad, with strongly convex sides.



FIGURES 1-8, *Pickfordiateuthis pulchella*, n.sp. Figure 1, holotype from Old Rhodes Key, Fla., 22 mm. mantle length; 2, paratype from Key Biscayne, Fla., 16.2 mm. mantle length, female; 3, paratype from Key West, Fla., 13.5 mm. mantle length, male; 4, dorsal sucker from third right arm; 5, ring from above; 6, lateral view of gladius from holotype; 7, dorsal view of gladius from holotype; 8, tentacular sucker ring of holotype.

The sides and posterior end curve in and downwards to form a protective shield for the body.

The viscera are enclosed in a thin transparent membrane which bears numerous, large, yellowish-brown chromatophores and beneath which the anatomy is plainly visible. The female from Key West was dissected and the accompanying figure (Fig. 17) was drawn from it. The entire posterior end of the mantle cavity was filled with large yellowish eggs about 1.9 mm. in diameter. The well-developed left oviduct with a single egg *in situ* is shown in Figure 18.

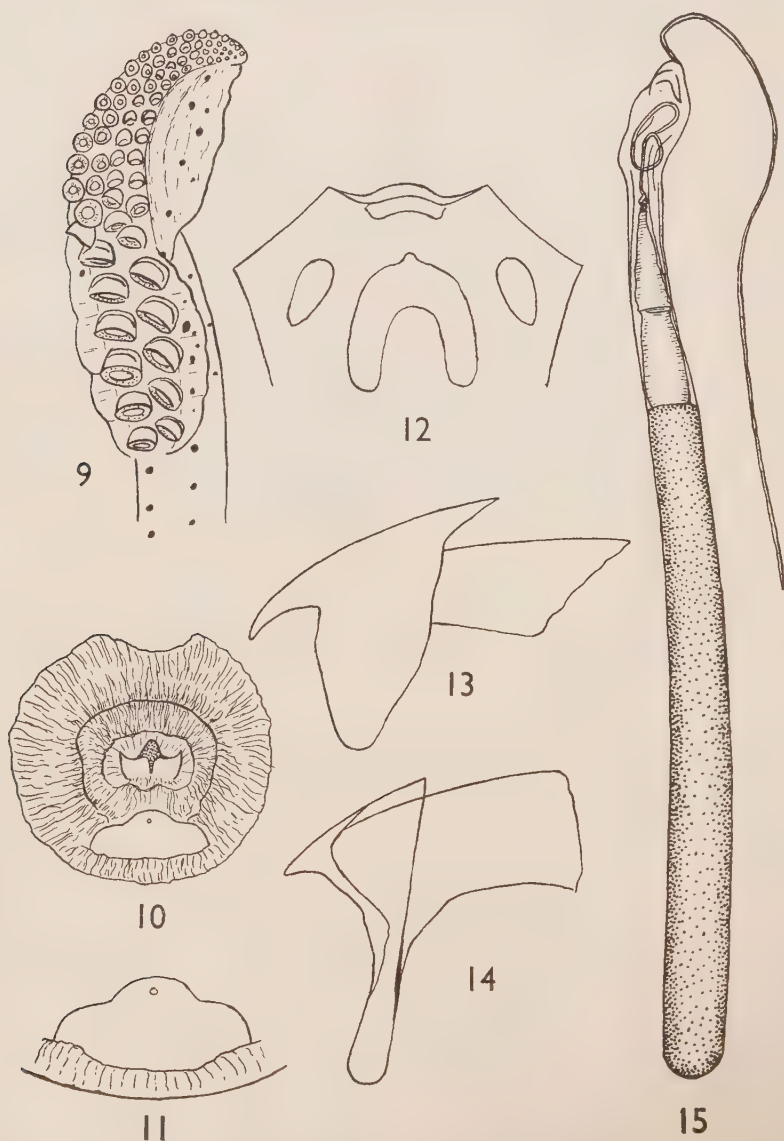
The buccal membrane (Fig. 10) is not lobed but has seven poorly developed supports. It is thick, closely folded and bears, in the female, a conspicuous, smooth, rounded spermatophore receptacle (Fig. 11) on the lower lip. The female from Key West had 27 spermatophores attached to the inner groove of the receptacle. A pit or pore is present in the central lobe but its function is not known. The mandibles are shown in Figures 13 and 14. The radula was not examined.

The funnel is strong, well-developed. The funnel organ (Fig. 12) consists of an inverted-U-shaped dorsal pad with a small round anterior projection. The paired ventral pads are oval, slightly tapered at their posterior ends. The funnel valve is semi-circular and strongly developed.

The small male from Key West was partially dissected to allow removal of several spermatophores from the penis. One of these is illustrated in Figure 15. It appears to be somewhat loliginid in structure.

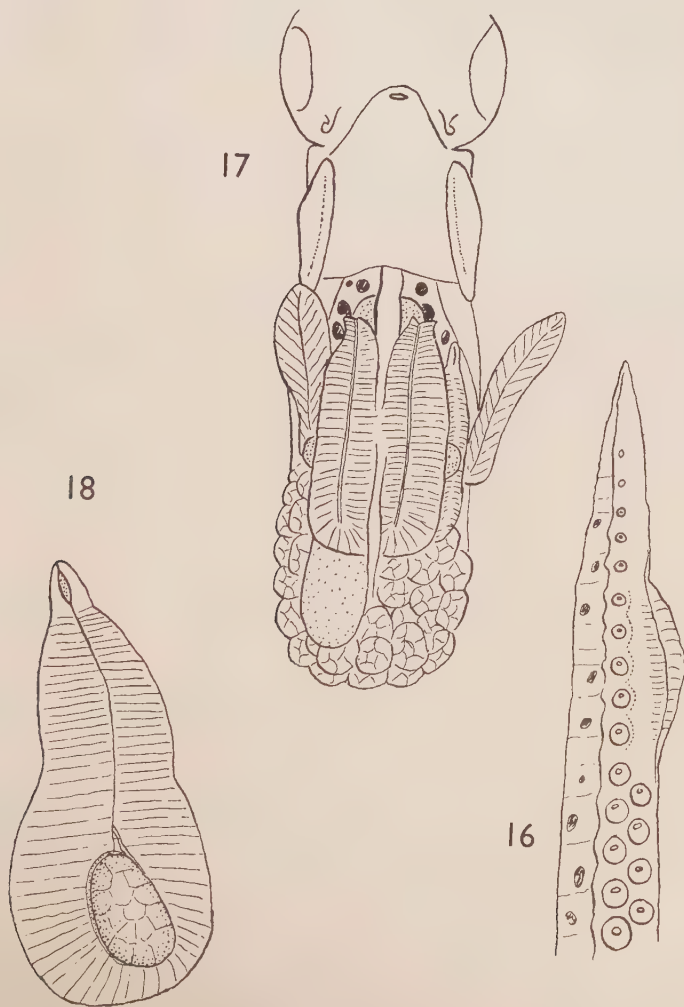
MEASUREMENTS (millimeters)
 OLD RHODES KEY KEY BISCAYNE KEY WEST
 (*Holotype*) (*Paratype*) (*Paratypes*)

Sex	F	F	M	F
Mantle length	22.0	16.2	13.5	17.0
Mantle width	10.0	6.5	6.1	7.5
Fin insertion	7.2	4.1	3.8	5.0
Fin length	11.2	8.5	7.0	8.5
Fin width	19.0	13.0	11.5	16.4
Head width	9.0	7.0	6.3	—
Arm length				
1st pair	7.0	4.0	3.0	—
2nd pair	8.5	6.5	6.2	—
3rd pair	10.0	7.0	7.0	—
4th pair	8.0	5.0	6.8	—



FIGURES 9-15, *Pickfordiateuthis pulchella*, n.sp. Figure 9, tentacular club showing arrangement of suckers, holotype; 10, buccal membrane and spermatophore pad from holotype; 11, details of spermatophore pad, showing pore; 12, funnel organ of holotype; 13, dorsal mandible from Key West female; 14, ventral mandible from Key West female; 15, spermatophore from Key West male.

Discussion. The author does not wish at present to enter into a discussion concerning the systematics of the myopsid squids. However, the formation of the new family Pickfordiateuthidae necessitates some remarks at this time concerning its relationships to other families of this group.



FIGURES 16-18, *Pickfordiateuthis pulchella*, n.sp. Figure 16, hectocotylized left ventral arm of Key West male; 17, general view of the internal anatomy of Key West female; 18, view of left oviduct with egg *in situ*, from Key West female.

Naef (1923) divided the Myopsida of d'Orbigny into two groups, the Metateuthoidea myopsida and the Sepioidea, the former containing only the families Loliginidae, Promachoteuthidae and Lepidoteuthidae, of which the last two are still of uncertain relationship. The Sepioidea contained all of the remaining families of the myopsida, including the Idiosepiidae which formerly were considered a connecting link between the Sepiolidae and the Loliginidae. Naef's two divisions were furthermore separated by the entire group of the Oegopsida.

Thiele (1935) retained the separate identities of Naef's groups but placed the Sepiacea, as he termed the Sepioidea, immediately preceding the Loliginacea. By this arrangement the old term Myopsida again becomes useable, if not preferred, in order to distinguish them from the Oegopsida.

At the present condition of our knowledge of the Pickfordiateuthidae it appears that this family may well be considered as a connecting link between the Sepiacea and the Loliginacea. In common with them, it has a transparent membrane over the eye, a well-developed and functional left oviduct, and other more obscure characters. It differs, however, from the Sepiacea in the lack of a secondary lid fold, and in the presence of a typical well-developed *Loligo*-like gladius entirely covering the viscera, non-retractile tentacles and a weakly developed *adductor pallii medianus*. On the other hand it differs from the Loliginacea in the unlobed buccal membrane without suckers, the lateral and ununited round fins and the presence of only two rows of suckers on the tentacular clubs instead of the usual four.

It thus appears to the author that the present family may well represent a connecting link between the Sepiolidae and the Loliginidae. On the other hand the possibility cannot be ignored that this family, with its strong loliginid affinities, may represent an offshoot from early loliginid stock, with only superficial resemblance to the Sepiolidae. Its true position will probably depend upon a close study of its embryonic and post-embryonic development.

Habitat. It is interesting to note that these small squids, mature as evidenced by the ripe eggs in the females and the spermatophores in the male, were taken in very similar habitats and from the full range of the Florida Keys. Thus it appears that they are shallow water coastal forms, living about the extensive flats covered with the marine grass *Thalassia testudinum*, which surrounds the shores of south Flor-

ida. The fact that they have escaped discovery until the present time may no doubt be explained by their extremely small size and the lack of all but cursory collecting in the area where they are found.

With the increase in our knowledge of the cephalopod fauna of the West Indian region, it is becoming increasingly evident that Florida and the Caribbean are part of a single faunistic area which also includes the Bermudas and all of the Antilles as far as the north coast of South America but excluding the Gulf of Mexico. However, in view of the extremely small size of this species, the large size of the eggs and its known habitat, it seems doubtful if it has more than a very short, if any, planktonic existence. This is borne out by the fact that no specimens have been taken in the numerous plankton hauls from the Florida Current between Florida and the Bahamas and off Key West. In view of the preceding facts it seems doubtful that this species will be found throughout the above area and probably it is confined to the geographical area represented by the Florida Keys.

Remarks. This new genus of myopsid squid was given the name *Pickfordiateuthis* in honor of Dr. Grace E. Pickford, who has contributed so greatly to our knowledge of the cephalopods of the West Indian Region. The trivial name *pulchella* refers to the small size and beautiful coloration of this remarkable new addition to our subtropical fauna.

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RESULTS OF HYDROGRAPHIC AND CHEMICAL INVESTIGATIONS IN THE REGION OF THE "RED TIDE" BLOOM ON THE WEST COAST OF FLORIDA IN NOVEMBER 1952¹

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ABSTRACT

Eleven hydrographic stations were occupied in the *Gymnodinium* bloom area off Fort Myers, Florida, in November 1952. These data provide the basis for a three-dimensional description of the hydrographic environment where the phenomenon occurred.

The current pattern in the area of study was more complex than is generally thought. There was eddying motion which appears to be seasonal in character.

Regions of maximum total phosphorus were found to coincide with water of Gulf origin, while water with greater river influence contained regions of minimum total phosphorus. This pattern implies that the increased phosphorus content probably came from the open Gulf.

The total phosphorus changed slowly with depth in a slanting water column, and areas of definite *Gymnodinium* bloom, while high in total phosphorus, did not coincide with areas of maximum observed total phosphorus which was some ten times the normal value.

Three mechanisms capable of effecting the observed total phosphorus pattern are given. No proven explanation of the causes of the recurrent plankton blooms is as yet available.

INTRODUCTION

From November 1946, to August 1947, sporadic blooms of *Gymnodinium brevis* (an unarmoured dinoflagellate), popularly known as the "Red Tide," occurred off the west coast of Florida, causing mass mortality of marine animals (Gunter, *et al.*, 1948; Galtsoff, 1948).

The blooming of *Gymnodinium* and concomitant mass mortality of fish recurred recently off the west coast of Florida. The first outbreak was reported off Fort Myers on November 11, 1952, and was on the decline a few days later. There were signs of another bloom off Dry Tortugas on January 3, 1953, and subsequent airplane observations disclosed suspicious areas. A definite recurrence was detected off Smith Shoal on January 22, 1953. This, too, was of brief duration. The localities are shown in Figure 1.

The Marine Laboratory of the University of Miami occupied eleven

¹ Contribution No. 90 from the Marine Laboratory, University of Miami. These studies were partly aided by a contract between the Office of Naval Research and the University of Miami, and partly by the Florida State Board of Conservation and the Gulf Oil Company.

hydrographic stations in the "Red Tide" area off Fort Myers in November 1952, and six hydrographic stations off Smith Shoal in January 1953. This paper reports on the hydrographic and chemical findings of the studies made in November only, as the data from the Smith Shoal region are still being processed.

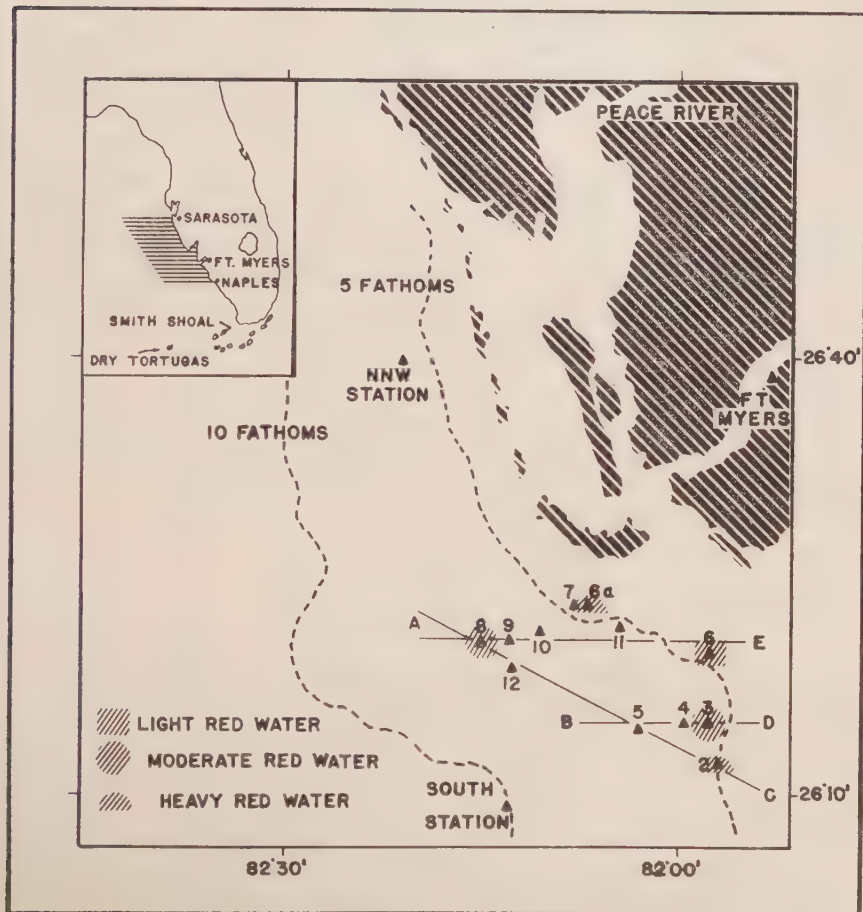


FIGURE 1. Locations of the 11 hydrographic stations (numbered 2 to 12), the detected red waters in the "Red Tide" region in November 1952, and the vertical sections shown in Figures 4, 5 and 6. Two stations occupied in 1949-1950 by Graham, *et al.*, are shown as NNW and South Stations. Inset map shows area of ocean covered by an airplane reconnaissance made in conjunction with the occupation of the 11 hydrographic stations.

The locations of the hydrographic stations are given in Figure 1. Stations were occupied over a period of three days. Long stops at each station were required for chemical and biological assays. Night work was considered impractical, since daylight was needed to locate "Red Tide" areas. The surface vessel was directed by an amphibious airplane which ranged as far as fifty miles off shore, flying as far north as Sarasota and as far south as Naples. If the visibility from the plane is taken as ten miles, the area covered by the plane was some 6,000 square miles (Fig. 1, hatched area in inset map). This two-day plane reconnaissance revealed only the five areas of definite red water marked on Figure 1.

It is a pleasure to acknowledge the contribution to this paper made by other members of the Marine Laboratory staff. James Murdock and Marvin Marks undertook the field work, with William Hess in charge. The work was under the general direction of P. F. Smith, with the able advice of F. G. Walton Smith. Robert Burrows identified the organism as *Gymnodinium brevis* Davis, and Sigmund Miller carried out the chemical analyses.

The Gulf Oil Company, at the suggestion of Mr. John Demerit, contributed financial support, and the Florida State Board of Conservation was the principal supporting agency.

The final manuscript was critically read by C. P. Idyll, H. B. Moore, F. G. W. Smith, P. F. Smith and R. H. Williams.

HYDROGRAPHIC RESULTS

The salinity patterns at two depths, surface and near the bottom (seven-meter depth) are given in Figures 2 and 3, respectively. A pocket of low salinity water with a minimum of 33.55 ‰ stood apart at the surface from a similar water mass nearer shore, and a high salinity tongue with a maximum of 34.38 ‰ occupied more than half of the area of investigation. At the surface along the western boundary of the area (Stations 8 and 12), the salinity gradient was the sharpest; it was some four times greater than the gradient in the high salinity tongue. To some extent, the corresponding total phosphorus gradient reflected this unequal spatial variation of salinity. As a whole this pattern, with its sharp western gradient, did not change appreciably with depth.

The temperature pattern (not reproduced) was similar to that of salinity. Regions of higher salinity were warmer than those of lower

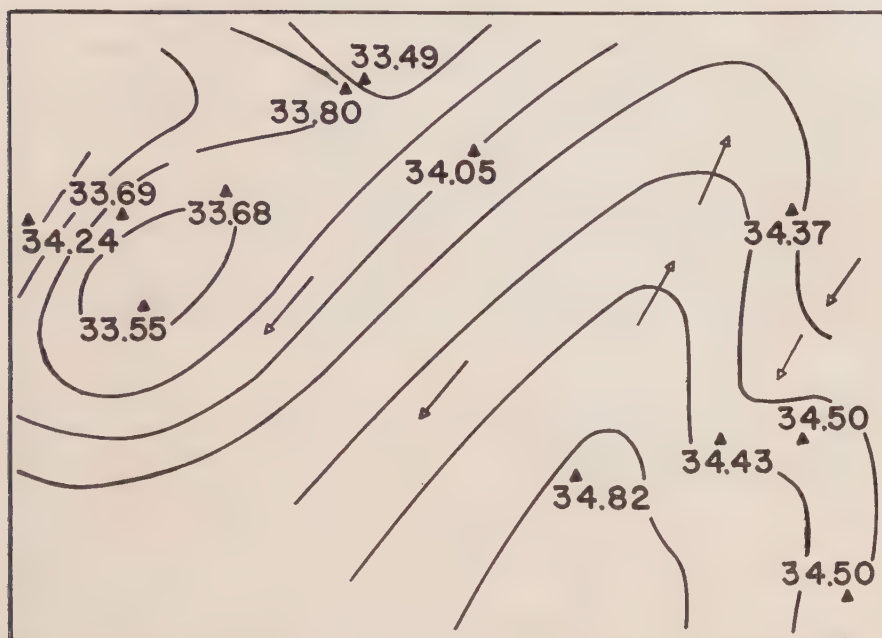


FIGURE 2. The distribution of surface salinity in parts per thousand. Arrows show probable current directions. Solid lines are isohalines drawn at intervals of 0.2 ‰.

salinity. However, the temperature gradient was smaller than the salinity gradient. This has its effect on the density of the waters and will be referred to later.

When the observed temperatures and salinities at each station are plotted on a temperature-salinity diagram, it will be seen that the water at Station 5 was the warmest and most saline, and the waters at Stations 6a, 7 and 12 were the coldest and the least saline, while the T-S curves of the waters at Stations 2, 3, 4, 6, 8, 9, 10 and 11 are seen to lie between the two extremes. This shows that the waters of intermediate temperature and salinity were produced by the mixing of the waters represented by those at Station 5 and at Stations 6a, 7 and 12. Further aspects of mixing will be discussed in a later paragraph. For ready reference, the warm saline water will be referred to subsequently as "Gulf water" and the cooler and less saline water as "river water."

The density values, plotted as Sigma-T in Figures 4 and 5, are obtained from the temperature and salinity data. Figure 4 is derived from data taken along Section A-B-C of Figure 1, and Figure 5, from

Section A-E. There are several features of interest in these sections. The absolute instability of the lower water column at Station 2, the zero stability at Station 11, and the columns of varying degrees of stability at the other stations, picture the process of intense mixing generally encountered in coastal areas with river runoff.

The current pattern can be obtained qualitatively from the Sigma-T sections. Quantitative results are impossible, since, in addition to the difficulty of finding a proper reference level, the neglected acceleration and friction terms in the geostrophic equation cannot be justified. The probable current pattern has been superimposed on the salinity pattern of Figure 2.

The inferred water movements in the present area of investigation illustrate the advective phase of the stirring and mixing processes considered by Eckart (1948). Referring to the effect of advection as stirring and the effect of diffusion as mixing, Eckart discussed the role of eddying motion as being very effective, not merely in increasing the mean gradient but also in increasing the interfacial area of the regions of different concentration and in decreasing the interfacial distance

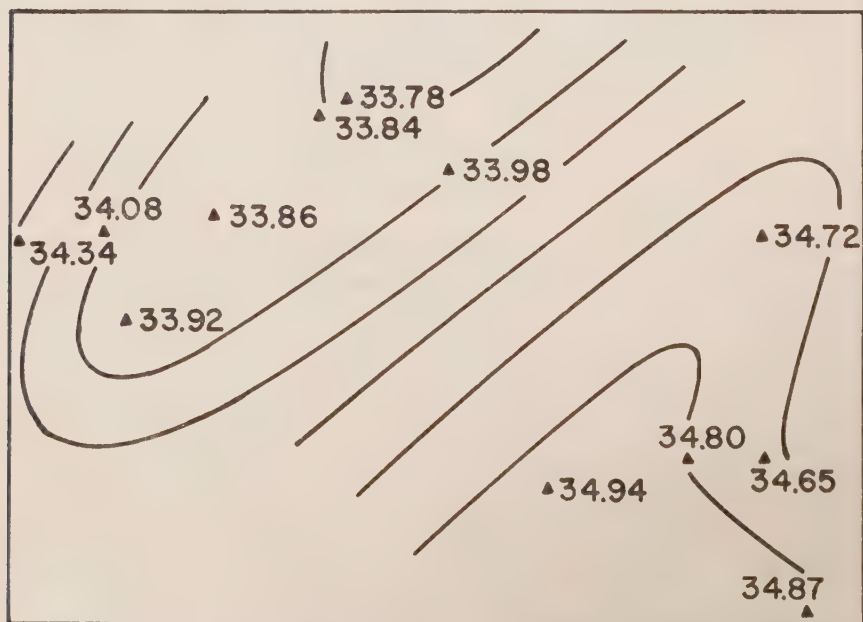


FIGURE 3. The distribution of salinity (‰) at the seven-meter depth. Isohalines are drawn at 0.2 ‰ intervals.

between them. Ordinarily, during the stirring stage these three advective processes dominate. Ultimately they may so increase the diffusion that the mixing process will dominate and cause the mean gradient to diminish toward zero.

The northerly current and the apparent southerly countercurrent in the present area of study seem to indicate eddying motion rather than motion due to local wind stress or boundary effect. Munk (1950) has shown that the countercurrents off California and the west coast of Mexico are caused by the curl of the meridional wind stress. However, no equivalent wind system exists off the west coast of Florida. The countercurrent between the Atlantic coast and the Gulf Stream has been interpreted as a boundary phenomenon by Sverdrup, *et al.* (1948, p. 677). A characteristic of this countercurrent is its continual existence throughout the year (see H. O. Pub. No. 571 for example) in contrast to the seasonal character of the California countercurrents. But charts of mean surface currents such as H. O. 10690, show no southerly currents whatever in the present area of study.

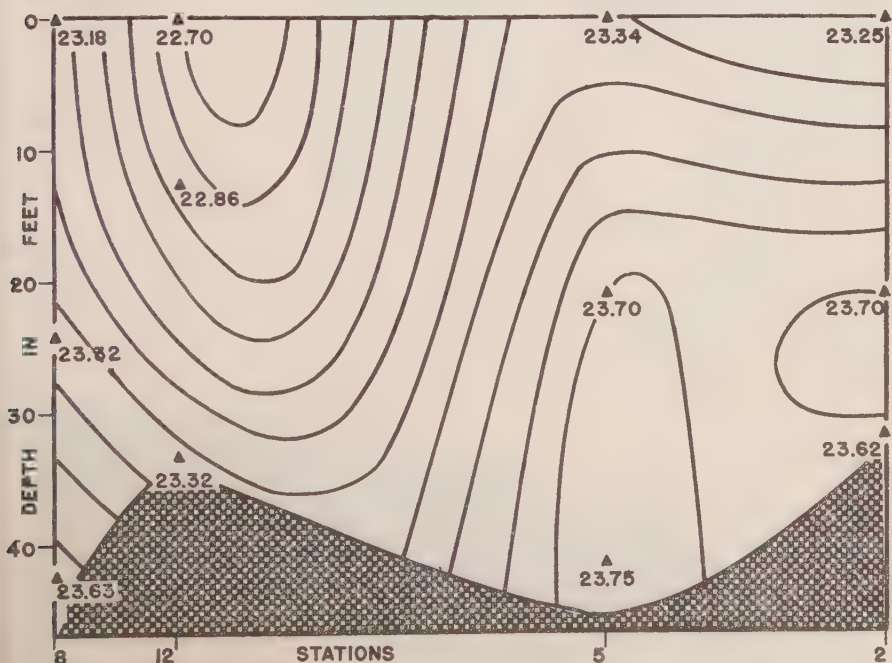


FIGURE 4. The distribution of Sigma-T (density) in a vertical section from A to C (location shown in Figure 1). Isolines are drawn at intervals of 0.0001 gm./cc.

Interpreting the interplay of northerly and southerly currents in the present area of study as a manifestation of eddying motion, the observed phenomena of the interdigitation of differing water masses, of the sharp salinity gradients and of the juxtaposition of the Gulf and river waters in the present area of study are readily seen as part and parcel of the stirring process. Ultimately the mixing process will dominate, and barring further river influx, the waters in the region will become homogeneous.

The total influx of the Caloosahatchee River into the area is highly seasonal. The maximum generally occurs in late summer or early autumn and the minimum in mid-winter. This seasonal character of the total influx is not appreciably affected by the controlled discharge of Lake Okeechobee into the Caloosahatchee River, because the volume of lake discharge in the winter is relatively small compared to the drainage resulting from the summer rainfall. As an illustration in

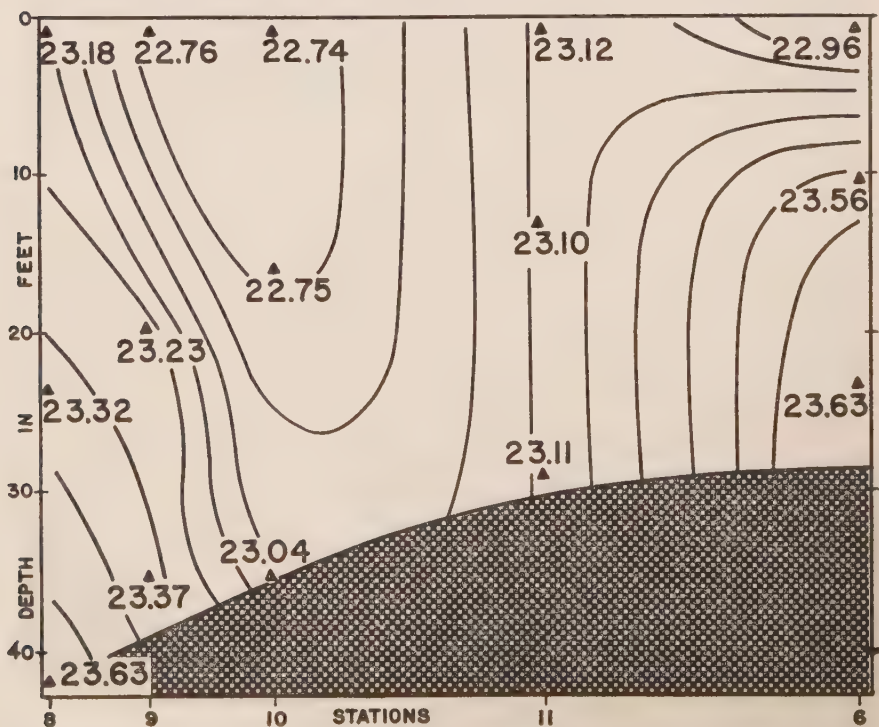


FIGURE 5. The distribution of Sigma-T (density) in a vertical section from A to E (location shown in Figure 1). Isolines are drawn at intervals of 0.0001 gm./cc.

point, the rainfall and lake discharge data for the years 1947 and 1950 may be examined. The data on the monthly lake discharge at the Moore Haven Lock at the source of the Caloosahatchee River were kindly furnished by Mr. K. M. Hartsfield, Corps of Engineers at Jacksonville, Florida. The rainfall data at four stations along the banks of the Caloosahatchee River were furnished by Mr. J. W. Hayes, U. S. Weather Bureau at Fort Myers, and by Mr. R. L. Anderson, U. S. Weather Bureau at Jacksonville, Florida. In the seven-year period beginning with January 1946, the discharge record shows that the largest monthly discharge occurred in December 1947; the volume was 150,990 day-second-feet or 13.8×10^9 cubic feet for the month.

The drainage into Caloosahatchee River resulting from rainfall may be estimated from the recorded rainfall at Fort Myers, La Belle, Moore Haven, and Ortona, all located along the banks of the river and somewhat evenly spaced. If it is assumed that the river drains the area within ten miles of its banks, then the drainage area is some 3.4×10^{10} square feet. The average monthly rainfall at the four stations was

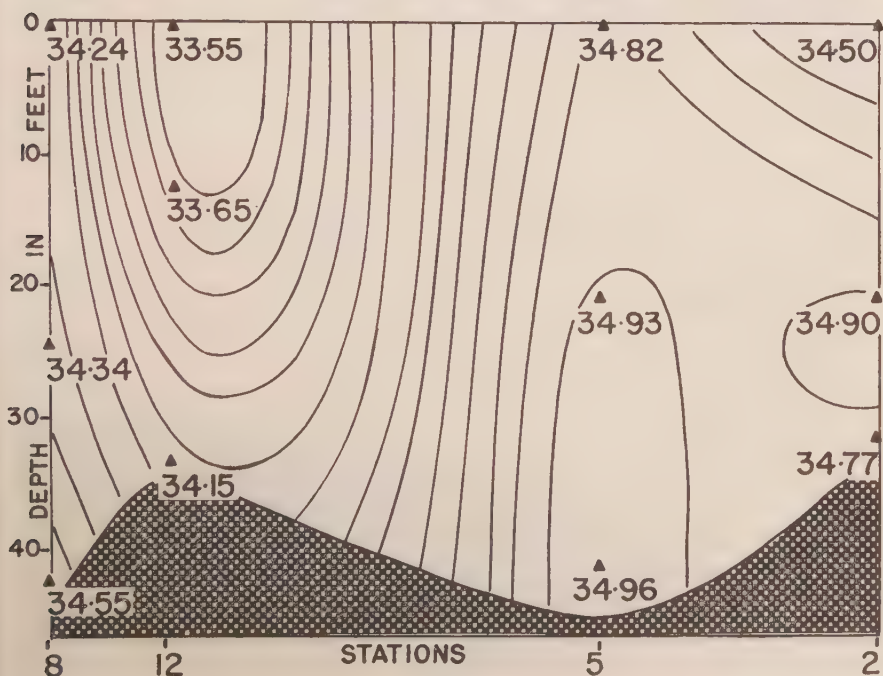


FIGURE 6. The distribution of salinity in a vertical section from A-B-C (location shown in Figure 1). Isohalines are drawn at intervals of 0.1 ‰.

1.2 feet in September 1947. Therefore the total volume of rain water drained by the Caloosahatchee River in that month was 40.8×10^9 cubic feet. Adding the corresponding lake discharge to the rainwater volume gives 46.8×10^9 cubic feet as the total volume emptying from the mouth of the river in September 1947. The corresponding total volume for December 1947 was 17.8×10^9 cubic feet. The summer maximum is found to be 2.6 times the winter minimum.

The total annual lake discharge in the same seven-year period was lowest in 1950 with the January discharge accounting for 85% of the total. This January discharge was 2.3×10^9 cubic feet, and the only other recorded discharge in the year occurred in May with a volume of 0.4×10^9 cubic feet. The rainfall volume for July 1950 was 18.7×10^9 cubic feet. Here, the summer maximal total runoff is 8.1 times the winter minimum.

If it can be assumed that the stirring process in the present area

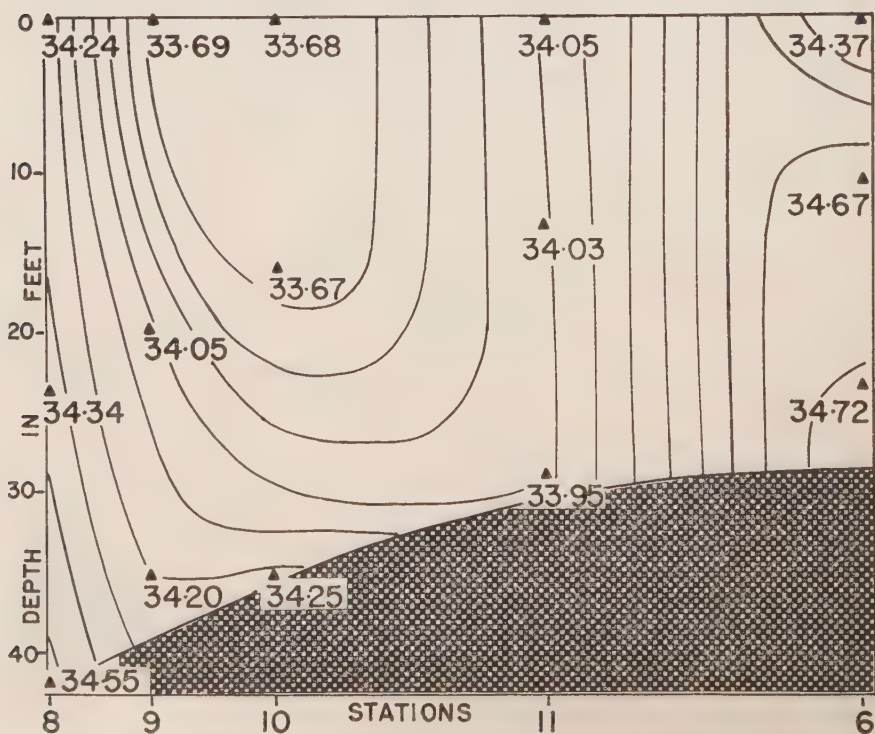


FIGURE 7. The distribution of salinity in a vertical section from A-E (location shown in Figure 1). Isohalines are drawn at intervals of 0.1 ‰.

progresses at a rate in direct proportion to the water volume drained by the Caloosahatchee River, then the seasonal character of the drainage would imply that the eddying motion is strongest and most persistent in the summer and weakest and least persistent in the winter. Hence the southerly currents inferred from the present data are inherently seasonal in character, in accordance with the fluctuation in river runoff.

The salinity pattern along the vertical sections A-B-C and A-E are given in Figures 6 and 7, respectively. On the whole these salinity and Sigma-T patterns (Figs. 4 and 5) are quite similar. This similarity implies that the variation of salinity was the determining factor in the differences in density between the Gulf and river waters. The lobe of Gulf water at Station 2, Figure 6, and the asymmetry of the pool of river water at Station 10, Figure 7, appear to be the results of differential advection, that is, there were vertical variations in the horizontal velocities.

CHEMICAL RESULTS

The water samples from the three depths of each of the eleven

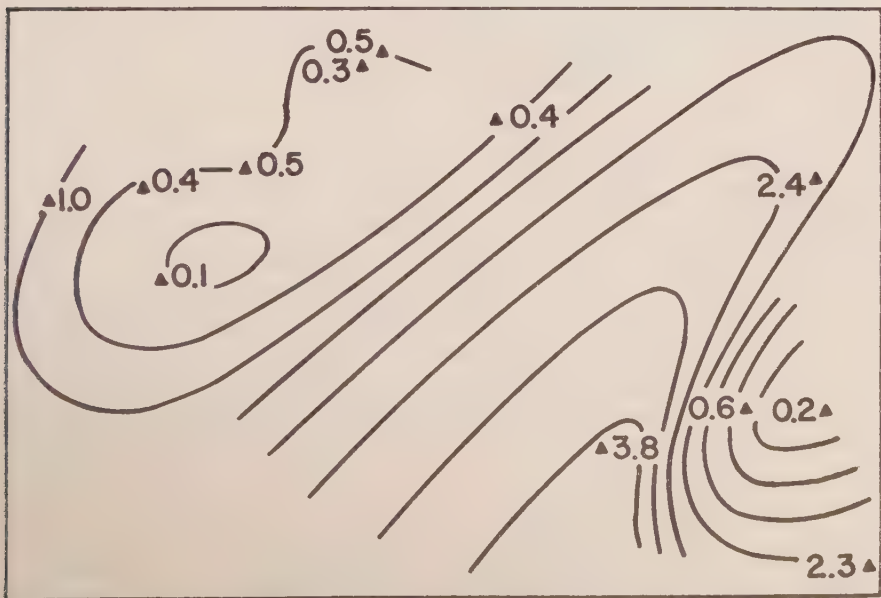


FIGURE 8. Total phosphorus ($\mu\text{g.-at./L.}$) pattern at the sea surface. Isolines are drawn at intervals of $0.5 \mu\text{g.-at./L.}$

stations were analyzed for total phosphorus. The method of Redfield, Smith and Ketchum (1937) was used and the accuracy is plus or minus $0.05 \mu\text{g.-at./L.}$ The results are plotted in Figures 8, 9 and 10 for the surface, seven-meter depth and the "near bottom," respectively. The regions of low total phosphorus coincided with those of river water, and the tongue of high total phosphorus, with that of the Gulf water at all depths. The observed high phosphorus tongue was displaced southeastward with depth, probably a result of the differential advection of Gulf water noted previously.

The highest total phosphorus, $3.8 \mu\text{g.-at./L.}$, was found at the surface at Station 5, in the middle of the tongue of northward thrusting Gulf water. From this high value the total phosphorus decreased vertically to $2.0 \mu\text{g.-at./L.}$ at the six-meter depth and thence to zero at the twelve-meter depth, or about eight feet from the bottom, indicating that the phosphorus was not uniformly distributed throughout the vertical water column. However, if the slanting column is followed from surface to bottom, it may be seen that the phosphorus content changed slowly with depth: it was 3.8 at the surface, greater than 2.0 at seven meters and greater than $1.5 \mu\text{g.-at./L.}$ at the bottom.

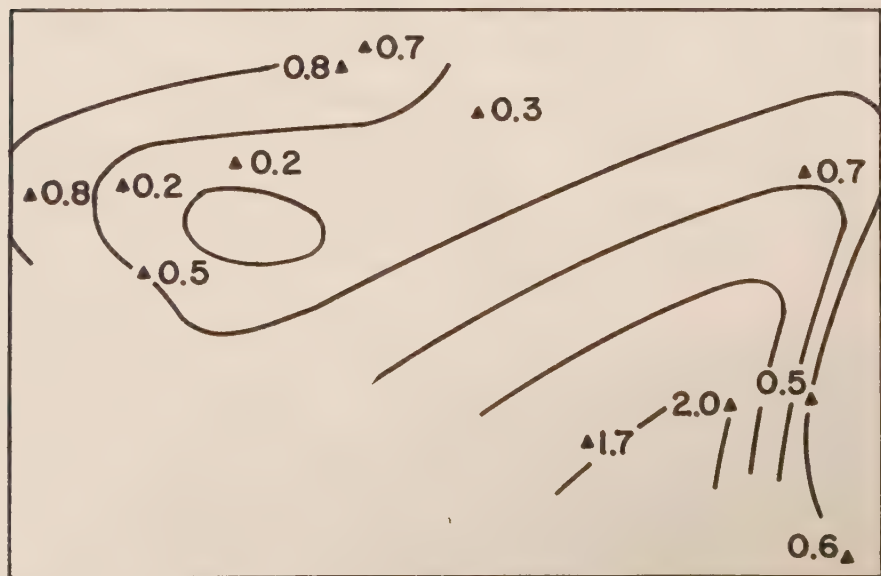


FIGURE 9. Total phosphorus ($\mu\text{g.-at./L.}$) pattern at the seven-meter depth. Isolines are drawn at intervals of $0.5 \mu\text{g.-at./L.}$

The dissolved inorganic phosphate content was determined to be below $0.03 \mu\text{g.}-\text{at.}/\text{L.}$ (Atkins-Denigés method used on board). This is low, but is in general accord with findings made elsewhere in water sustaining large plankton blooms (Sverdrup, *et al.*, 1946, p. 259).

For all water columns in the present area of study, the oxygen content showed values exceeding saturation; one sample was over 200% (Table 1). A significant distribution pattern of the dissolved oxygen is the plot of the means of the three individual oxygen determinations at each station. It will be seen that this oxygen distribution conforms closely to that of the salinity. The more saline Gulf water is seen to contain greater amounts of dissolved oxygen than the less saline river water. This pattern strongly suggests that the supersaturation was caused not by intense and persistent mixing at the water-air interface but by high photosynthetic activity in conjunction with a high phytoplankton content.

DISCUSSION

The total phosphorus for the 16-month period from May 1949, to August 1950, for two stations just outside the area of this study, is given by Graham, *et al.* (1953). One station is some twenty miles north-northwest of Station 8 of the present study, and the other is some fifteen miles south of it. At the one-meter depth, the following total phosphorus content ($\mu\text{g.}-\text{at.}/\text{L.}$) was found:

	Mean	Range
North-northwest Station	0.71	0.20 - 1.60
South Station	0.18	0.15 - 0.20

According to Graham, *et al.*, the high value at the NNW station was due to unusual circumstances: "During the hurricane of August, 1949, a slime dam containing phosphate sludge at one of the mines broke, releasing large quantities of phosphate . . . The high value . . . is probably related to this . . ." Taking 0.50 as an estimated mean for the NNW station with the unusual effect eliminated, the average of the values of the two stations may perhaps be taken as a normal value of total phosphorus for this region. This estimated value is $0.34 \mu\text{g.}-\text{at.}/\text{L.}$

The highest total phosphorus value found in the present investigation in this area is $3.8 \mu\text{g.}-\text{at.}/\text{L.}$, some ten times the normal value, but only about one-fifth of the $20.4 \mu\text{g.}-\text{at.}/\text{L.}$ value found by Ketchum and Kean (1948) in the 1946-1947 "Red Tide." Almost the entire tongue of Gulf water contained values of total phosphorus

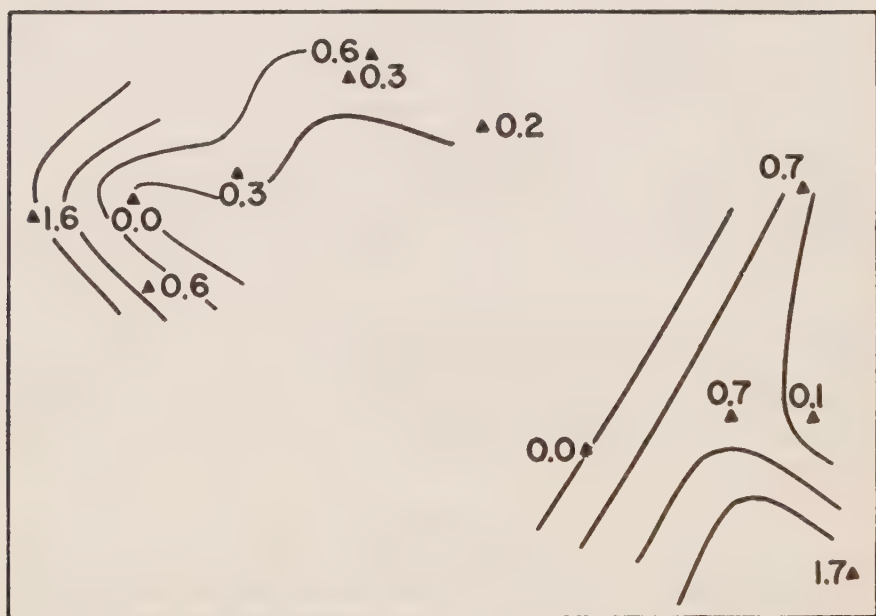


FIGURE 10. Total phosphorus ($\mu\text{g.-at./L.}$) pattern at a depth close to the bottom (see Table 1 for exact depth). Isolines are drawn at intervals of $0.5 \mu\text{g.-at./L.}$

greater than the normal, while as a whole, the river water contained values less than the normal. This was true for all depths. It would appear that phosphorus was being diffused from the Gulf water into the river water at all depths at the time of observation.

The significance of the identification of low total phosphorus with river water and of high total phosphorus with Gulf water seems unmistakable. The increased phosphorus content appears not to have come from river runoff; instead it seems very likely to have come from the region from the open Gulf.

The fundamental cause or causes of "Red Tide" still remain to be discovered, but our present investigations have delineated the problem in clearer terms. The hypothesis of bottom leaching suggested by Smith (1948) remains a possible mechanism capable of supplying the high phosphorus content observed. If the submarine deposits of mineral phosphates were at a distance offshore, then if leaching did occur, the pattern of phosphate distribution would be similar to that found.

TABLE I

TEMPERATURE, TOTAL PHOSPHORUS, SALINITY, AND OXYGEN VALUES AT THE ELEVEN HYDROGRAPHIC STATIONS OCCUPIED IN NOVEMBER 1952, OFF FORT MEYERS, FLORIDA.

Station (No.)	Date Nov.	Time (EST)	Depth (M.)	Temp. (°C.)	Total Phosphorus ($\mu\text{g-at./L.}$)	Salinity (‰)	Oxygen (% Sat.)
2	14	1451	0	24.13	2.3	34.50	168.9
2	14	1451	6	23.61	0.3	34.90	177.9
2	14	1451	10	23.55	1.7	34.77	151.6
3	15	1127	0	23.84	0.2	34.50	178.1
3	15	1127	5	23.37	0.7	34.51	163.6
3	15	1127	10	23.42	0.1	34.88	150.4
4	15	1240	0	24.12	0.6	34.43	176.8
4	15	1240	5	23.46	2.8	34.78	172.3
4	15	1240	10	23.53	0.7	34.82	150.7
5	15	1338	0	24.61	3.8	34.82	190.5
5	15	1338	6	23.70	2.0	34.93	179.1
5	15	1338	12	23.59	0.0	34.97	157.8
6	15	1600	0	24.76	2.4	34.37	228.6
6	15	1600	3	23.50	0.0	34.67	198.2
6	15	1600	7	23.37	0.7	34.72	157.9
6a	16	1154	0	23.44	0.5	33.49	159.2
6a	16	1154	3.9	23.32	1.1	33.78	130.1
6a	16	1154	7.9	23.10	0.6	33.78	140.9
7	16	1234	0	23.40	0.3	33.80	162.0
7	16	1234	4.9	23.26	1.3	33.81	163.7
7	16	1234	8.9	23.07	0.3	33.86	139.8
8	16	1408	0	23.67	1.0	34.24	185.1
8	16	1408	7	23.46	1.2	34.34	161.6
8	16	1408	12.9	22.95	1.6	34.55	127.9
9	16	1510	0	23.69	0.4	33.69	190.5
9	16	1510	6	23.02	0.2	34.05	149.9
9	16	1510	10.9	22.93	0.0	34.20	106.9
10	16	1655	0	23.75	0.5	33.68	142.0
10	16	1655	5	23.69	0.1	33.67	190.7
10	16	1655	10.9	22.93	0.3	34.25	125.1
11	16	1225	0	23.40	0.4	34.05	120.8
11	16	1225	3.9	23.43	0.5	34.03	114.3
11	16	1225	8.9	23.17	0.2	33.96	106.2
12	16	1407	0	23.55	0.1	33.55	137.3
12	16	1407	3.9	23.27	0.4	33.65	132.0
12	16	1407	9.8	22.98	0.6	34.16	101.7

Graham, *et al.* (1953) found that concentration of the blue-green alga *Trichodesmium* by winds and tide into long bands constitutes a mechanism for the local accumulation of large quantities of phosphorus, and that should conditions become unfavorable for the survival of this organism, a large quantity of organic matter would be-

come available to the biological cycle in the sea. This mechanism could lead to a phosphate pattern similar to that observed if a sequence of events, such as the following, is postulated. First, the winds and currents (individually or in combination) concentrate the *Trichodesmium* some distance offshore. Subsequently, this organism dies and releases a great mass of organic matter into the water; decomposition and regeneration of the inorganic substances follow. Suppose now that there exist the optimal physical and biological environments, including the presence of sufficient *G. brevis*. A *G. brevis* bloom would then appear, locally or over large areas. These areas become death traps to many marine animals, entering from outside regions, which on death decompose to enrich the water with nutrients. The biological cycle goes on as phytoplankton utilize the nutrients and are themselves in turn utilized by other organisms. In other words, a *G. brevis* bloom area is thought of as a mechanism to concentrate organic and thence inorganic substances into the whole water column as it moves toward shore.

H. B. Moore (personal communication) suggests another possible mechanism capable of accounting for the high phosphorus content found. He postulates a zone of surface convergence offshore, concentrating a wide area of plankton into a relatively narrow zone. The sinking water in the convergence zone is thought to leave no advective effect on the swimming dinoflagellates, which remain near the surface. When the convergence zone is advected toward the shallow continental shelf, the surface layer would fill the whole water column. There are no data at present to test any of these hypotheses, and a certain explanation of the causal factors leading to a "Red Tide" bloom is not yet available.

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Instructions for Preparation of Manuscripts

CONTRIBUTIONS will be considered which deal with research in the marine sciences, directly or indirectly related to the southeastern United States and the Caribbean area. Papers dealing solely with the economic or applied aspects of commercial fisheries will not be accepted.

Manuscripts may be submitted in languages other than English but publication will be in English only. Where possible, arrangements will be made for translation.

All copy should be typewritten and double spaced. Footnotes should be avoided as far as possible. If used they should be numbered continuously throughout the paper and set off in the body of the text.

Bibliographical references must be indicated by author's name and year of publication. References should be listed under that heading in alphabetical order of authors. Each reference should include the last name followed by initials or the first name. Co-authors should be listed with initials preceding the last name. The date should appear next to the author's name, followed by a complete title, in lower case except for the first word. The publisher, city and pagination should follow, in the case of books. The names of periodicals should be abbreviated as in "World List of Scientific Periodicals," Oxford. The volume is then given in arabic numerals underlined for italics, followed by the number in brackets and the pagination preceded by a colon. After the first line of each reference the copy is indented.

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TABLE OF CONTENTS

	PAGE
1. HILARY B. MOORE: Plankton of the Florida Current. II. Siphonophora	559
2. L. B. ISHAM AND J. Q. TIERNEY: Some aspects of the larval development and metamorphosis of <i>Teredo</i> (<i>Lyrodus</i>) <i>pedicellata</i> De Quatrefages	574
3. SAMUEL P. MEYERS: Marine fungi in Biscayne Bay, Florida	590
4. GILBERT L. VOSS: A new family, genus and species of myopsid squid from the Florida Keys	602
5. FRANK CHEW: Results of hydrographic and chemical investigations in the region of the "Red Tide" bloom on the west coast of Florida in November 1952	610

